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Temperate-climate myxomycetes in Australia and the Southern Hemisphere

Peter Wellman

17 Warragamba Avenue Duffy ACT 2611
wellmanp@iinet.net.au

***Abstract*:** The paper present the results of a new field collection of myxomycetes (plasmodial slime moulds) on dead wood, dead bark and litter substrate in southeast New South Wales centred on Canberra (lat. 35° S, long. 149° E). The sample consists of 96 species from 493 collections. This survey is compared with four other surveys for similar substrates and similar temperate climate: southwest Western Australia, southeast Australia, New Zealand and Patagonia. The assemblages are similar in species composition and abundance, when allowance is made for the large random effect in the sampling. These five southern hemisphere assemblages have been combined into a composite assemblage. This composite assemblage is similar to those of the Iberian Peninsula (Spain and Portugal) and Britain, when allowance is made for the varying sampling of litter. This similarity may represent a single species assemblage occurring in both the Southern and Northern Hemispheres in areas of similar temperate climate.

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Introduction

Myxomycetes (plasmodial slime moulds) are a small group of fungus-like organisms with a two-stage life cycle; a single nucleate phase (amoeboid or flagellated), and a multinucleate (single cell) phase starting as a plasmodium and ending as a fruiting body (containing spores) generally 0.5-2 mm high. Identification is based on the dried fruiting body.

Pre 1995 records of Australian myxomycetes are listed by Mitchell (1995). Subsequent papers on myxomycetes on wood, on bark of dead logs, on dead bark on living trees, and on litter are reported by Ing & Spooner (1994), McHugh et al. (2003), Black et al. (2004), Jordan et al. (2006), Rosing et al. (2007), Davison et al. (2008) McHugh et al. (2009), Knight and Brims (2010), Lloyd (2014), Wellman (2015), Davison et al. (2017) and Wellman (2015, 2016). Myxomycetes on liana material are reported by Wrigley de Basanta et al. (2008), and those associated with snowbanks by Stephenson and Shadwick (2009). Many of these papers primarily increase the known species in Australia, and its states. As a result of these and other studies there is a reasonable species list for Australia. The list is weak mainly in central and northern Australia, and for species on litter.

The next stage in understanding the myxomycetes in Australia is finding the myxomycete species associations in each myxomycete province for each type of substrate. For each species association we need a large enough sample to obtain a reliable species list, with information on the relative importance of each species. This has been addressed to some extent by Wrigley de Basanta et al. (2008) for moist chamber cultures from lianas in tropical rain forests, Stephenson and Shadwick (2009) for the snowbank species, Knight and Brims (2010) for field collection on wood and bark substrate in temperate WA, and by Wellman (2015, 2016) for moist chamber cultures of dead bark across Australia.

Myxomycetes can be collected either by finding and collecting mature fruiting bodies in the field (field collection), or by collecting potential myxomycete substrates that may have spores and/or dormant structures (microcysts), growing the myxomycetes in the laboratory and identifying fruiting bodies that are produced (moist chamber culture). This paper is about myxomycetes obtained by field collection.

Australian myxomycetes are most often collected in the field on dead wood and bark. Analysis of this information is difficult as the species list is long (about one quarter of the myxomycetes species for the World), the species range from rare to common, and their occurrence is variable in time and space. To analyse this data it is necessary to have large samples to allow for random sampling effects. The main object of this paper is to analyse Australian temperate collections with new survey data from SE New South Wales, and compare these results with other temperate areas in the Southern and Northern Hemispheres.

Sampling sites and methods

The collections reported here were from the Australian Capital Territory (ACT) and adjacent south eastern New South Wales (NSW), centred on the city of Canberra (latitude 35° S, longitude 149° E) (Fig. 1). The area is a highland 'plateau' at about 600 m, with some incised gorges, and higher forested ranges to about 1200 m altitude, and a narrow coastal lowland strip 100 km to the southeast. Most of the collections were made within 60 km of Canberra, but a few were made on the coastal strip 150-200 km to the south and to the northwest. The area has a temperate climate. Average rainfall is about 600 mm per year on the plateau, with a higher rainfall to above 1000 mm per year in the higher forested mountains, and on the low altitude coastal strip and its bounding escarpment east of Canberra. Long-term average rainfall is fairly uniform throughout the year, but in any year there can be long periods of weeks or months with no significant rainfall. Most of the wooded area is eucalypt dry sclerophyll forest, with small areas of wet sclerophyll forest, temperate rainforest, or cool rainforest.

In dry sclerophyll forest myxomycetes fruiting bodies can usually be found by field collecting in autumn, and sometimes in late spring or summer. Few fruiting bodies are seen through the winter and early spring because it is too cold. Field collection was carried out a week or more after a suitable rainfall provided that, in the period after the rain, the temperature was not too high and humidity not too low. A forested area was found of suitable dryness; generally the mountains receive more rain, there is more shade, and the moisture evaporates more slowly. At any altitude the northwest slopes had a relatively dry forest while the southeast slopes had a relatively wet forest. Because many fallen trees and branches are difficult to lift because of their mass, much collecting concentrated on logs and branches that had fallen on tracks and roads and been subsequently cut up and moved into the forest, or in areas where there has been complete felling of the *Eucalyptus* or *Pinus radiata* forest in the last few years, but no burning of the residue. Myxomycete fruits are generally found a week or more after rain, on the shaded bottom half of the wood or bark, the last portion that is damp. All species that were found on a site were collected.

In spring and summer the main fruiting events are initiated by 10-50 mm rainfall, separated by weeks or months of none or minor rainfall, but relatively high temperatures and low humidity. Dry sclerophyll forest is in an environment where the common trees (*Eucalyptus* species) provide only 30% shade. Hence dead wood, bark and litter is very dry for much of the warmer half of the year. Most trees are evergreen with relatively thick rigid leaves, so the ground litter of leaves and twigs is packed loosely on the ground, and dries out relatively quickly after rain. Because of the above factors it is relatively easy to collect fruiting bodies of myxomycetes that occur on dead wood or dead thick bark, but relatively difficult to collect those that occur on damp litter. Myxomycetes on litter substrate were collected attached to dead wood/bark where this was close or touching compacted litter (for example on sites 927, 928, 930, 931, 932), with fruiting bodies on bark of the introduced cork oak (*Quercus suber*) where it is resting on its leaves (sites 926, 929), on flood debris of *Casuarina cunninghamiana* wood/bark, in needles and twigs with fruiting bodies on the wood/bark, and sites 917 and 922 with a mixture of *Eucalyptus* branches, leaves and twigs graded off the road with myxomycete fruiting bodies on the wood and leaves.

Field collection sampling may be biased towards species that are obvious (large, brightly coloured, or in a prominent position), or towards species that fruit in the autumn, but against species that occur on litter.

Identification of the dried myxomycete fruiting bodies was carried out mainly using Ing (1999), Stephenson (2003), Poulain et al. (2011), and the website 'Discover Life' (2016). Temporary microscope slides were made by soaking the material in alcohol and 5% KOH solution. Microscope slide mounts of many species were made to study the stalk, peridium, capillitium, and inflated spores by soaking the fruiting body in alcohol, then in 5% KOH solution, in water, and then in 'Brite' mountant (a USA furniture polish used for liverwort slides), and covering with a cover slip. Mounts of members of the Stemonitaceae were made by blowing spores off the fruiting body and putting it horizontally in the air space of a cavity slide. It was not possible to identify some fruiting bodies that were few in number, not mature, or partly colonized by fungi.

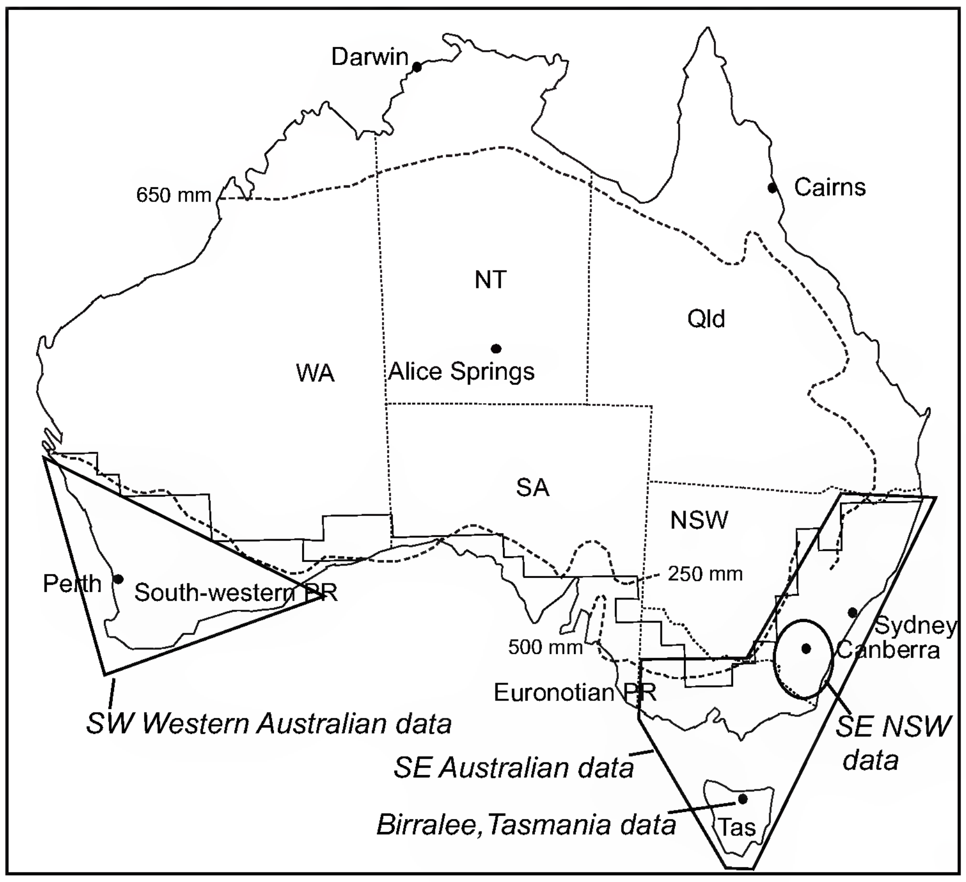

Figure 1. Location of the myxomycete collections. Field samples are discussed for the areas shown – Birralee-Tasmania, SW of Western Australia, SE New South Wales and SE Australia. The extent of the temperate climatic region is thought to be the area of the Euronotian and Southwestern Phytogeographic Provinces, limited approximately by contours of 250 mm and 500 mm mean annual rainfall.

Table 1. Species list for southeast New South Wales

The table lists the myxomycete species found, and their sites. The records are tabulated in Table 2 column 3. Western Victorian site 897* is in Table 2 column 4.

Arcyria affinis Rostaf, 931, 1091.

Arcyria cinerea (Bull.) Pers, 725, 753, 768, 821,856, 903, 907, 911, 913, 920, 924, 925, 926, 936, 943, 950.

Arcyria denudata Fr, 684, 903, 929.

Arcyria incarnata (Pers ex J. F Gmel) Pers., 897*, 901, 906, 914, 915, 920, 931, 951.

Arcyria insignis Kalchbr & Cooke, 750, 756, 855, 889, 911, 925, 950.

Arcyria obvelata (Oeder) Onsberg., 821, 832, 856, 897*, 901, 903, 911, 920, 923, 929, 942, 954, 1091.

Arcyria oerstedii Rostaf., 889, 891, 918, 923.

Arcyria pomiformis (Leers) Rostaf., 856, 920, 926.

Arcyria virescens G. Lister, 916.

Badhamia panacea (Fr.) Rostaf., 926.

Ceratiomyxa fruticulosa (Müll.) Mac., 715, 716, 784, 815, 842, 856, 889, 897*, 901, 903, 906, 911, 917, 918, 922, 944, 941, 950, 1092.

Clastoderma debaryanum A. Blytt., 953.

Comatricha alta Preuss., 924, 929.

Comatricha elegans (Racib) G. Lister, 917.

Comatricha ellae Härk., 911, 913, 906, 913 cf.

Comatricha laxa Rostaf., 856, 905, 920, 927.

Comatricha nigra (Pers ex J. F Gmel) J. Schröt., 856, 857, 889, 906, 911, 912, 919, 922, 923, 929.

Comatricha pulchella (C. Bab) Rostaf., 753, 754, 757, 856, 889, 913 aff, 918, 923.

Comatricha subalpina M. L. Farr et S. L Stephenson, 753, 901 cf, 906 cf.

Comatricha vineatilis Nann, -Bremek., 917.

Craterium minutum (Leers) Fr., 673.

Cribraria argillacea (Pers ex J. F Gmel) Pers., 760.

Cribraria cancellata (Batsch) Nann –Bremek., 815, 848, 856, 907, 909, 915, 925, 942, 943, 925, 954.

Cribraria intricata Schrad., 815.

Cribraria microcarpa (Schrad) Pers., 906, 914, 926, 929, 942, 946.

Cribraria mirabilis (Rostaf) Massee, 941, 943.

Cribraria rufa (Roth) Rostaf., 948.

Cribraria splendens (Schrad) Pers., 650, 731, 848, 897*, 909, 918, 923, 944.

Cribraria vulgaris Schrad., 856, 923.

Diacheopsis "parvula" 889 (see Poulain et al. 2011).

Dianema corticatum Lister, 751.

Diderma hemisphaericum (Bull) Hornem., 929.

Diderma radiatum (L.) Morgan, 897*.

Didymium minus (Lister) Morgan, 926.

Didymium nigripes (Link) Fr., 932.

Didymium squamulosum (Alb & Schwein) Fr., 915, 923, 926, 930, 932.

Enerthenema papillatum (Pers) Rostaf., 856, 859, 929.

Fuligo septica (L.) F. H. Wigg., 767, 903, 929, 943, 946, 1093.

Hemitrichia intorta (Lister) Lister, 919, 921 cf.

Hemitrichia leiocarpa (Cooke) Lister, 897* cf, 906, 917, 922, 923.

Hemitrichia serpula (Scop) Rostaf ex Lister, 1091.

Lamproderma arcyrionema Rostaf., 901, 906, 911, 924, 925.

Lamproderma scintillans (Berk & Broome) Morgan, 897*.

Leocarpus fragilis (Dicks.) Rostaf., 930.

Lycogala epidendrum (J. C. Buxb. ex L.) Fr., 784, 814, 856, 859, 903, 924, 945.

Metatrichia floriformis (Schwein) Nann –Bremek., 889, 924, 926, 929, 929, 952, 953.

Oligonema schweinitzii (Berk) G. W Martin, 746.

Paradiachea cylindrica (Bilgram) Hertel ex H. Neubert, Nowotny & K. Baumann, 898.

Paradiacheopsis fimbriata (G. Lister & Cran) Hertel ex Nann – Bremek., 915.

Physarum album (Bull) Chevall, 897*, 909, 911, 913, 914, 953.

Physarum bivalve Pers., 927, 928, 930, 932.

Physarum cinereum (Batsch) Pers., 723, 728, 856, 888, 910, 922, 926, 955.

Physarum compressum Alb, & Schwein, 932.

Physarum contextum (Pers) Pers., 756.

Physarum decipiens M. A. Curtis, 915, 920 cf.

Physarum flavicomum Berk., 679, 784, 846, 906, 907, 909, 912, 918, 922, 924, 925, 929.

Physarum globuliferum (Bull) Pers., 944, 941, 948.

Physarum leucophaeum Fr., 902, 922, 925, 929 943.

Physarum megalosporum T. Macbr., 858.

Physarum notabile T. Macbr., 888.

Physarum oblatum T. Macbr., 944 cf.

Physarum pusillum (Berk & M. A Curtis) G. Lister, 922.

Physarum vernum Sommerf., 932.

Physarum viride (Bull) Pers., 730, 741, 751, 768, 888, 897*, 902, 906, 907, 909, 911, 912, 913, 914, 917, 920, 922, 923, 925, 929, 941, 942, 943, 948, 1093.

Reticularia liceoides (Lister) Nann –Bremek., 857 cf.

Reticularia lycoperdon Bull., 930, 931.

Reticularia olivacea (Ehrenb) Fr., 856.

Reticularia splendens Morgan, 901, 904, 913 cf.

Stemonitis axifera (Bull). T. Macbr., 726, 733, 814, 856, 901, 903, 911, 913, 918, 929, 944.

Stemonitis flavogenita E. Jahn, 913.

Stemonitis fusca Roth, 676, 746, 784, 808, 823, 850, 897*, 903, 911, 920, 923, 947, 950, 1092.

Stemonitis herbatica Peck, 733, 906, 913, 922.

Stemonitis splendens Rostaf., 891, 894, 897*, 902, 906, 926, 929, 944, 949, 1092.

Stemonitopsis amoena (Nann -Bremek) Nann –Bremek., 908, 911.

Stemonitopsis typhina (F. H Wigg) Nann –Bremek., 717, 722, 756, 806, 814, 899, 903, 908, 929,942, 943, 950, 1090, 1093.

Trichia affinis de Bary, 751, 764, 889, 897*, 917, 950.

Trichia botrytis (J. F Gmel) Pers., 818, 824, 893, 925, 952, 953, 954.

Trichia contorta (Ditmar) Rostaf, 932.

Trichia decipiens (Pers.) T. Macbr., 1899. 925, 926, 929, 942, 922 cf, 889.

Trichia erecta Rex, 764.

Trichia persimilis P. Karst, 822, 952.

Trichia scabra Rostaf, 899.

Trichia varia (Pers.) Pers., 684, 744, 750, 754, 756, 848, 888, 927, 929, 953.

Trichia verrucosa Berk., 677, 719, 720, 744, 745, 761, 762, 764, 806, 815, 816, 818, 819, 820, 824, 842, 849, 901, 906, 915, 942, 1091.

Tubifera arachnoidea Jacq., 743, 760, 889.

Willkommlangea reticulata (Alb & Schwein) Kuntze, 917, 931.

Results

Table 1 lists the species identified. *Ceratiomyxa fruticulosa* has been included in the following text and tables although it is in Ceratiomyxaceae. Appendix 1 gives the localities where collections were made.

Extent of the temperate climatic area assemblage of myxomycetes in Australia

The geographic extent of any temperate field collection myxomycete species assemblage cannot be defined by the field collection records, because the records are very sparse near its likely boundary. However traverses across Australia looking at the myxomycetes found by moist culture of dead bark (Wellman, 2016) shows that in NSW the boundary between the temperate and southern arid region assemblages corresponds to the Euronotian/Eremaean Phytogeographic Region boundary, and, to the north, the boundary between other assemblages corresponds to other phytogeographic region boundaries, where these boundaries are from González-Orozco et al. (2014). Hence the most likely extent of the temperate region is one which corresponds to the Euronotian Phytogeographic Region in NSW, Victoria, Tasmania and South Australia, and to the South-Western Phytogeographic Region in Western Australia (Fig. 1). This temperate boundary follows a climatic boundary - the 500 mm mean annual rainfall contour in NSW, and the 250 mm mean annual rainfall contour in South Australia and Western Australia (Fig. 1).

Southern Hemisphere species lists

The extent of the various Australian collections is shown in Figure 1. Table 2 columns 1 to 5 summarize the Southern Hemisphere assemblages of temperate myxomycetes from field collections on dead wood, bark on dead wood and litter. The numbers give abundance estimates from collections or provinces. The following genera have not been included because their fruiting bodies are of small size, so that they are unlikely to be adequately sampled in field collections: *Echinostelium, Licea, Paradiacheopsis,* and *Macbrideola,* except *Macbrideola oblonga*.

Table 2. Species assemblages from field collection in temperate climates.

Column 1, near Birralee, Tasmania, from Lloyd (2014), modified in a few details (pers. comm). **Column 2**, SW Western Australia, from Knight and Brims (2010). **Column 3**, SE New South Wales, (from Table 1). **Column 4**, SE Australian data in Australian Herbaria (Australia's Virtual Herbarium, 2016). **Column 5**, New Zealand, (Stephenson, 2003). **Column 6**, Patagonia and Tierra del Fuego, Argentina, South America (Wrigley de Basanta et al., 2010). **Column 7**, Total Southern Hemisphere temperate. Sum of columns 2-6. **Column 8**, Iberian Peninsula, Europe (Lado 1991). **Column 9**, Britain, Europe (Ing, 1999). **Unit in body of table**: **x**, present; **C**, collection; **P**, province; **‰**, number of collections or provinces per 1000. ##, in columns 8 and 9 not all species are listed. *, species that may live partly or wholly on litter. #, *Diderma radiata*; two sites in Tasmania (S.L. Stephenson UARKM 19974, 6482), and one site in Western Victoria - locality 897. **SH**: southern hemisphere **NH**: northern hemisphere

Country	Australia				NZ	Arg		Ibe	Bri
Hemisphere	SH						SH	NH	NH
Column	1	2	3	4	5	6	7	8	9
Area	Tas	WA	SE NSW	SE her	NZ	Pat	SH	## Ibe	## Bri
Collecting unit	C	C	C	C	P	C	‰	‰	‰
Latitude	41	30 35	35 37	33 39	35 47	40 55	30 55	40 51	50 56
Alwisia lloydiae	x								
Arcyria affinis	x	1	1	1	4		4	3	3
Arcyria cinerea	x	11	22	9	11	3	29	14	13
Arcyria denudata	x	3	3	8	10	4	15	14	13
Arcyria ferruginea	x	2		2	3	1	4	8	9
Arcyria glauca	x								
Arcyria globosa			1				0.5	2	
Arcyria incarnata	x	4	8	3	7	1	12	16	13
Arcyria insignis		1	8		3	1	7	1	0.1
*Arcyria major**					1		0.5	3	1
Arcyria minuta		5			1		3	2	3
Arcyria obvelata	x	11	13	7	6	2	21	14	13
Arcyria occidentalis		1					0.5		
Arcyria oerstedii			4		3		4	5	6
Arcyria pausiaca		4					2		
Arcyria pomiformis	x	11	11	2	4	1	15	11	13
Arcyria riparia	x								
Arcyria stipata		2			1		2	1	2
Arcyria virescens			1		2		2		
Badhamia affinis			1	2			2	3	4
*Badhamia apiculospora**					1		0.5		0.3
Badhamia capsulifera		1			2		2	1	5
*Badhamia foliicola**	x	5		7	2		7	14	6
Badhamia goniospora		1					0.5	1	
Badhamia panicea		1					0.5	3	
*Badhamia macrocarpa**					2		1	3	4
*Badhamia melanospora**					1		0.5		
Badhamia nitens	x				3		2		3
Badhamia panicea			1				0.5	3	11
Badhamia utricularis	x	1	1		5		4	9	12
Badhamia versicolor		1	1			1	2	2	2
Badhamia viridescens	x								0.2
Badhamiopsis ainoae			1				0.5	2	0.1
Calomyxa metallica	x	1	4		3	1	5	3	9
Ceratiomyxa fruticulosa	x	10	17	9	16	4	29	11	13
Clastoderma debaryanum	x	4	3		5		6	1	0.7
Colloderma oculatum		2			1		2	2	9
Colloderma robustum	x								
Comatricha alta	x		2	2	2		3	5	5

Column	1	2	3	4	5	6	7	8	9
Area	Tas	WA	SE NSW	SE her	NZ	Pat	SH	## Ibe	## Bri
Comatricha elegans	x	19	9		1		15	7	
Comatricha ellae		9	9	2			11	3	1
Comatricha laxa	x	2	6		3	1	6	7	7
Comatricha longipila		1					0.5		0.8
Comatricha mirabilis									0.1
Comatricha nigra	x	5	11	1	7	15	21	19	13
Comatricha pulchella		2	9		2		7	2	11
Comatricha pulchelloides		1					0.5		
Comatricha rigidirecta		1					0.5		1
Comatricha subalpina	x		3				2		
Comatricha tenerrima		1		1			1	1	7
Comatricha vineatilis		1	2		1		2		
*Craterium aureum**		1			2		2	3	7
*Craterium leucocephalum**		2			1		2	10	9
*Craterium minutum**	x	2	1	1	11		8	8	13
*Craterium obovatum**					2		1		
Cribraria argillacea		1	1		2		2	6	13
Cribraria aurantiaca		1			3	1	3	4	13
Cribraria cancellata	x	9	11	2	8	2	17	9	13
Cribraria dictydioides					1		0.5		0.4
Cribraria intricata			1	2	2		3	1	3
Cribraria macrocarpa	x			1	3		2		2
Cribraria microcarpa		3	6	2	4	1	8	3	1
Cribraria mirabilis		1	2		1		2	1	2
Cribraria persoonii					1		0.5	2	9
Cribraria rufa		3	1			2	3	1	11
Cribraria splendens			7	1	1		5	1	1
Cribraria stellifera cf			2				1		
Cribraria tenella		2					1		2
Cribraria violacea		2	4	1	2		5	3	3
Cribraria vulgaris			2	4	2		4	5	1
*Diachea leucopodia**		12		2	9		12	1	8
Diachea radiata		1					0.5		
*Diacheopsis depressa**					1		0.5		
Diacheopsis 'pavula'			1				0.5		
Dianema corticatum		1	7		2		5	1	2
Dianema depressum	x				2		1	1	3
Dianema harveyi					1		0.5	3	2
Dictydiaethalium	x								
Dictydiaethalium plumbeum	x		1	1	5		4	6	9
Diderma antarcticum						1	0.5		
Diderma asteroides		2		2	2		3	6	1
Diderma chondrioderma				1	2		2	1	4
Diderma cinereum		1		1	1		2	2	0.2
Diderma crustaceum	x	1		2			2		
Didrma deplanatum								1	5
*Diderma donkii**					1		0.5		1
*Diderma effusum**		1		5	2	1	5	3	8
Diderma globosum					1		0.5	3	5
Diderma gracile						5	3		
*Diderma hemisphaericum**		1	1		2		2	5	7
*Diderma miniatum**					1		0.5		
Diderma ochraceum					1		0.5		4

Column	1	2	3	4	5	6	7	8	9
Area	Tas	WA	SE NSW	SE her	NZ	Pat	SH	## Ibe	## Bri
Diderma peyerimhoffi						1	0.5		
Diderma radiatum#				3		1	2	2	2
Diderma robustum						2	1		
Diderma saundersii		1					0.5		
*Diderma spumarioides**				2	1		2	9	7
*Diderma testaceum**					1		0.5	1	2
*Didymium anellus**		1			1		1	3	3
Didymium applanatum	x								0.2
*Didymium bahiense**	x	3		1	5		5	6	
Didymium clavus	x	1		1	3		3	8	10
*Didymium difforme**		5	2	2	5	1	8	13	13
*Didymium dubium**		1		2	2		3	5	1
*Didymium iridis**					1		0.5	2	12
*Didymium megalosporum**		1			6		4		3
Didymium minus			1			2	2	6	5
*Didymium nigripes**	x		1	2	5	1	5	10	13
Didymium perforatum		1					0.5		0.1
*Didymium serpula**		3			1		2	2	4
*Didymium squamulosum**	x	4	7	5	11		14	20	13
Didymium verrucosporum		1					0.5	3	1
Elaeomyxa cerifera	x			2			1	1	0.1
Elaeomyxa reticulospora	x								
Enerthenema papillatum	x	11	16		3		16	9	13
Erionema aureum					1		0.5		
*Fuligo cinerea**		2			2		2	6	2
Fuligo megaspora		1					0.5		0.1
Fuligo septica	x	20	5	39	20	9	49	17	2
Hemitrichia calyculata		1			3		2	1	10
Hemitrichia clavata					1		0.5	5	5
Hemitrichia intorta	x		2				1	1	1
Hemitrichia leiocarpa	x		4	1	2		4	1	0.1
*Hemitrichia minor**		1			3		2	3	6
Hemitrichia serpula					7		4	1	0.3
Hemitrichia velutina	x								
Lamproderma arcyrionema		3	6	1	2	1	7	3	7
Lamproderma collinsii		1					0.5		
Lamproderma columbinum	x			3	2		3		10
Lamproderma echinulatum	x				5	1	3		2
Lamproderma elasticum	x								
Lamproderma						1	0.5		
Lamproderma scintillans		2	0	2	2		3	6	11
*Leocarpus fragilis**	x	8	1	9	7	4	15	14	13
Lepidoderma crassipes				1			0.5		
Lycogala conicum		1					0.5		1
Lycogala epidendrum	x	15	7	16		6	23	25	13
Lycogala exiguum				1	1		1	1	1
Lycogala flavofuscum					3		2	3	3
Macbrideola oblonga		2					1	1	
Metatrichia floriformis	x	4	7		17	12	21		13
Metatrichia vesparium					3		2	5	7
*Mucilago crustacea**	x			1	2		2	14	12
Oligonema flavidum						1	1	1	1
Oligonema schweinitzii		4	1				3	1	4

Column	1	2	3	4	5	6	7	8	9
Area	Tas	WA	SE NSW	SE her	NZ	Pat	SH	## Ibe	## Bri
Paradiachea caespitosa	x	1					0.5		
Paradiachea cylindrica			1				0.5		
Perichaena chrysosperma			1		1	1	2	3	9
Perichaena corticalis		8		1	2		6	7	12
Perichaena depressa		8		1	4	1	7	6	8
Perichaena pedata						1	0.5		1
Perichaena quadrata				1			0.5		
Perichaena vermicularis	x	3	9		2		7	10	5
Physarum album	x	2	5	4	10	5	14	18	13
*Physarum bitectum**		2			2		2	6	6
*Physarum bivalve**		1	5	4	3		7	8	11
*Physarum bogoriense**	x				2		1	1	
*Physarum braunianum**					1		0.5	4	
*Physarum cinereum**		7	7	4	19	1	20	8	10
Physarum citrinum		1			1		1		3
*Physarum compressum**	x	4	2	2	5		7	6	9
Physarum conglomeratum		1					0.5	2	2
Physarum contextum			1				0.5	3	4
Physarum daamsii		1					0.5		
Physarum decipiens		1	3		1		3	6	2
Physarum dictyospermum					1		0.5		
Physarum didermoides					1		0.5	1	3
Physarum famintzinii		1					0.5		
Physarum flavicomum	x		13		3		8	1	
Physarum globuliferum	x		3	2	3		4	1	1
*Physarum gyrosum**					2		1	1	
*Physarum honkongense**					1		0.5		
Physarum lateritium					2		1		1
Physarum lenticulare cf			1				0.5		
Physarum leucophaeum		1	4	1	11	1	9	9	13
*Physarum leucopus**					2		1	3	3
*Physarum licheniforme**					2		1		
Physarum limonium					1		0.5	1	1
Physarum luteolum	x	1					0.5	2	
Physarum megalosporum			1				0.5		
*Physarum melleum**		3		1	3		4	3	
Physarum notabile	x				1		0.5	1	0.5
Physarum nucleatum					1		1		1
Physarum nudum		1					0.5	2	0.2
*Physarum obscurum**					2		1		2
Physarum pezizoideum					2	1	2	4	
*Physarum pusillum**	x	8	1		8		9	8	6
Physarum robustum		1	2		1		2	4	7
Physarum serpula					1		0.5	2	
Physarum sessile		1					1	1	0.2
*Physarum straminipes**		1			2		2	5	3
Physarum vernum		2	1		3	1	4	6	5
Physarum virescens			1				0.5	1	8
Physarum viride	x	23	29	8	14	5	42	6	13
Prototrichia metallica	x				2		1	2	5
Reticularia intermedia		1					0.5		3
Reticularia jurana						5	3		10
Reticularia liceoides			1		2		2		2

Column	1	2	3	4	5	6	7	8	9
Area	Tas	WA	SE NSW	SE her	NZ	Pat	SH	## Ibe	## Bri
Reticularia lycoperdon		2	3	1	4		5	15	13
Reticularia olivacea		1	3				2	3	1
Reticularia splendens			3				2	2	
Stemonaria irregularis				1			0.5		
Stemonaria longa				1			0.5		0.1
Stemonitis axifera	x		12	6	11	9	20	5	12
Stemonitis flavogenita			1	1	1	2	3	4	12
Stemonitis fusca	x	6	13	14	8	11	27	15	13
*Stemonitis herbatica**	x		4	1	4		5	3	6
Stemonitis laxifila		1					0.5		
Stemonitis lignicola	x	3				1	2	1	2
Stemonitis marjana	x								
Stemonitis pallida	x				2		1	1	
Stemonitis smithii		1			1		1	2	2
Stemonitis splendens	x	4	10	1	8	1	13	3	1
Stemonitis virginiensis		2		1	1		2	8	2
Stemonitopsis amoena		2	4				3	2	2
Stemonitopsis gracilis	x	2					1		1
Stemonitopsis hyperopta	x				2		1	2	9
Stemonitopsis peritricha		1					0.5		
Stemonitopsis reticulata		1					0.5		0.1
Stemonitopsis typhina	x	6	13	3	8	1	16	6	13
Symphytocarpus					1		0.5	1	5
Symphytocarpus trechisporus	x								
Trichia affinis	x	8	6	2		18	18	3	13
Trichia botrytis	x	2	8		6	3	10	6	13
Trichia brimsiorum				1			0.5		
Trichia contorta		4	2	2	3	5	8	8	8
Trichia crateriformis					1		0.5		
Trichia decipiens	x	12	9	3	9	13	24	10	13
Trichia erecta			1	1	2		2		
Trichia favoginea		12		3	13	11	21	6	2
Trichia flavicoma						3	2	2	4
Trichia lutescens					3	3	3	3	2
Trichia munda		1		1			1		5
Trichia persimilis		9	2			4	8	3	13
Trichia scabra			1		3		2	5	10
Trichia varia	x	6	10	2	11	1	16	14	13
Trichia verrucosa	x	3	21	11	14	12	32	1	5
Tubulifera arachnoidea	x	4	3	5	8	2	12	8	13
*Willkommlangea reticulata**	x	4	2		5	3	7	2	2

Table 2, column 1. The Tasmanian data of Lloyd (2014) from near Birralee, with a few changes in identification. The data set is very important because it records many species on litter not recorded by other collectors. There are 79 species reported. The collections were all from the field, within 1 km of a house, throughout the year, in the period 2010-2014. They are from a range of forest types, all relatively wet. No abundance information is published.

Table 2, column 2. The Western Australian data is that given by Knight and Brims (2010). The abundance measure given is the number of samples in the herbarium given by Knight and Brims (2010). There are 131 species and 452 records. It is possible that some of these records are from moist culture, but the proportion is small. The herbarium documentation does not distinguish between field collection and moist culture samples.

Table 2, column 3. The SE NSW data is that discussed above. There are 96 species and 493 records.

Table 2, column 4. The SE Australian Herbarium data is that given for the temperate area within Victoria, ACT, Tasmania and NSW in Australia's Virtual Herbarium (2016), with the addition of site 897 in western Victoria from this paper. There are 79 species and 256 records.

Table 2, column 5. The New Zealand data are from Stephenson (2003). There are 153 species and 573 province records. The data set is the best in the Southern Hemisphere in relation to the number of samples, the number of collectors, and the number of years of collecting. The measure of abundance used is the number of provinces for which a species has been reported, as the number of collections is not easily obtained. The effect of using provinces rather than collections is to decrease the relative abundance for the commoner species relative to the rarer species, but the exact effect is unknown so a correction has not been applied.

Table 2, column 6. The Patagonian and Tierra del Fuego data from Argentina are from Wrigley de Basanta et al. (2010). There are 61 species and 216 records. The combined sample is rather small. It is biased to species fruiting over the short collecting time from late January to early February in 2005. The species collected from the two areas are similar, so the data from Tierra del Fuego have been included although it is of much higher latitude (55°S) than any other Southern Hemisphere survey areas.

European species lists

To identify differences and similarities between the temperate field survey species assemblages of the Southern and Northern Hemispheres a suitable Northern Hemisphere data set would have abundance data, be based on 2000 or more records, be collected over a wide range of ecological sites over many years, and be similar to the Southern Hemisphere areas in mean latitude and climate. The best data sets I could obtain are of the Iberian Peninsula (Spain and Portugal), and of Britain. The Southern Hemisphere, Iberian and Britain data sets are listed in Table 2, columns 7, 8 and 9, with the relative abundances expressed as abundance per thousand (collection or province) of the total species assemblage.

Table 2, column 7. This is a Southern Hemisphere temperate mean species assemblage. It is the sum of columns 2-6 expressed as records per thousand. The number of collection/province records is 2170 for the Southern Hemisphere.

Table 2, column 8. The Iberian Peninsula (Spain and Portugal) data used is that of Lado (1991). This dataset contains a small proportion of samples obtained by moist culture (Pando and Lado, 1990). The proportion is less than 80 in 1552 collections (<5%), and is unlikely to affect any of the conclusions given below. There were many collectors of field collection myxomycetes. They cover a large area, with many different habitats, and collected over many years. The range of latitude is 36-44°N, and the range in annual rainfall is generally 400-1000 mm. The measure of species abundance used is the number of provinces where the species has been recorded, out of a total of 59 provinces. The average climate is not a good match for the southern temperate climate as much of the area is too arid. However, most of this collection will be from the wetter areas within the Peninsula bounding ranges and from ranges rising above the plateau, because of the difficulty of field collecting in arid areas.

Table 2, column 9. The species assemblage of Britain is from Ing (1999). The collections are very large in number, the climate and terrain is relatively uniform, and the records cover a long period. The measure of species abundance used is the number of Watsonian vice-counties (the geographical framework for much biogeographic recording in the UK) for which the species has been recorded. There are 8400 vice-county records, over 112 vice-counties. Although this data set is mainly that of field collections, it is likely to have a small proportion of moist culture collections. The range of mean annual rainfall is generally 600-1000 mm, and the summer is relatively cool.

Discussion

Within Southern hemisphere data sets (Table 2 columns 1 to 6) there is reasonable agreement between which species are present, and which are common or rare. This similarity is consistent with the areas being in one Southern Hemisphere temperate 'province' with a uniform species composition.

There are 78 species found in the Southern Hemisphere but not in the Iberian Peninsula, while 84 species found in the Iberian Peninsula have not been found in the Southern Hemisphere. The only common species in the Southern Hemisphere not recorded in the Iberian Peninsula is *Metatrichia floriformis*. Species not yet found in the Southern Hemisphere but which are relatively common in the Iberian Peninsula are: three species which probably have not been collected because their physical appearance is unusual for a well preserved myxomycete (*Amaurochaete atra* (5‰), *Lindbladia tubulina* (6‰) and *Symphytocarpus flaccidus* (4‰)), and five other species: *Comatricha lurida* (5‰), *Diderma trevelyanii* (3‰), *Diderma umbilicatum* (4‰), *Didymium trachysporum* (4‰), and *Hemitrichia abietina*

(4‰). Five species are not very many, and the abundance of these species in the Iberian Peninsula is low. Hence the Southern Hemisphere assemblage is very similar to the Iberian assemblage, with similar species relatively abundant.

The species occurring in the Southern Hemisphere and Britain are remarkably similar. Species that do not occur in Britain are generally rare (1-2‰) in the Southern Hemisphere; except *Diderma gracile* (3‰), *Physarum melleum* (4‰) and *Physarum flavicomum* (8‰). Species that do not occur in Southern Hemisphere but occur in Britain are generally rare in Britain, or species found in an environment poorly collected in the Southern Hemisphere - e.g. tree stumps, and litter. Exceptions to this are *Cribraria piriformis* (9‰), *Diderma floriforme* (5‰), *Lycogala confusum* (3‰), *Lycogala terrestre* (8‰), and *Physarum psittacinum* (6‰). This English data set is very similar in abundant species to the Southern Hemisphere assemblage.

It is not believed that the numbers per thousand for the Southern Hemisphere in Table 2, give the exact abundance of species the field as there is a bias towards samples that are obvious (large, brightly coloured, or in a prominent position) such as *Fuligo septica* (36‰) and *Physarum viride* (35‰). There is also a bias against common, identifiable species such as *Ceratiomyxa fruticosa* which is easily recognized in the field but may not be collected because they are not significant, so that its collected abundance is lower than its actual abundance (Stephenson, 2003). In addition, both in herbarium collections, and in surveys where all species in a locality are collected, there is a bias towards uncommon species. The most commonly seen species have an abundance of 20-25‰ (eg. *Ceratiomyxa fruticulosa, Comatricha nigra, Metatrichia floriformis, Trichia decipiens, Trichia favoginea, Trichia verrucosa*), and species found only once in the Southern Hemisphere have an abundance of 0.5‰ (eg. *Paradiachea cylindrica, Lamproderma collinsii*), giving a ratio of 50:1. This ratio is believed to be far too low; the common species have a much higher relative abundance in the field. In part this is thought to be due to the common species not being adequately collected, and in part due to some of the uncommon species actually being of lower real abundance than in the table, they just happened to be collected. However these comments about the accuracy of the mean abundance are comments about detail; it is believed that the numbers do reflect their relative (but not absolute) abundance in the field.

The combined Southern Hemisphere species assemblage can be used to address the question of whether there are any species that are more common in the Southern than the Northern Hemisphere. *Trichia verrucosa* is very common in the forest of New Zealand (Stephenson, 2003) and southeast New South Wales, and in all the Southern Hemisphere temperate areas except southwest Western Australia (Table 2); so compared with the sparse distribution in the Northern Hemisphere in Discover Life (2015), there is strong evidence that it is more common in the Southern Hemisphere.

There are two extreme models of myxomycete species distribution and their abundance within a climatic zone (assuming a suitable substrate is available). In one model all species do not necessarily occur over the whole extent of the zone and their relative abundance may vary over the zone (varying assemblage); in the other model the species and their abundance is constant within the zone and there are abrupt boundaries at the climatic zone margins (constant assemblage). There is evidence to support both models. Evidence for a varying assemblage is given by distribution maps such as those for Britain and Ireland (Ing, 1982). Evidence for a constant assemblage is given by a study of corticolous myxomycetes on a 3300 km long traverse across Australia, where four species assemblages were found (with transition zones between), each assemblage being constant in composition along its traverse length (Wellman, 2016). If the main effect was that of the varying assemblage, then the rather different average climates of each of the seven species assemblies of Table 2 would result in each area being different in dominant species and their abundance. This does not appear to be so. I think the similarity in the assemblages (in Table 2) is support for the constant assemblage model, with the same temperate assemblage occurring both in the Southern and Northern Hemispheres. However, there are likely to be a few species more common to different regions.

Although the data sets are robust enough for qualitative comparisons, they are not sufficiently uniform in structure to use a statistical comparison. The main limitations are the abundance data not having the same frequency distribution, and the relatively poor sampling of litter substrate species in Spain and the Southern Hemisphere.

Conclusions

1. I present the results of collections of myxomycetes in southeastern New South Wales. These are field collections for wood and bark substrate giving 96 species from 493 collections.

2. Details of six independent collections of field collection myxomycetes from temperate areas of the Southern Hemisphere are tabulated. For the five surveys with an abundance measure, mainly dead wood and bark substrate, the observed species abundances are in rough agreement when allowance is made for a large random sampling error. The rough agreement is consistent with a single temperate species assemblage for the dead wood and bark substrate occurring at each of these five locations. In these five data sets the species that grow on a litter substrate have largely not been collected. The litter species are better represented in the sixth collection from northern Tasmania obtained in a relatively wet forest.

3. The combined data set of the five Southern Hemisphere assemblages is similar to that of the Northern Hemisphere Iberian Peninsula (Spain and Portugal) and Britain, which have similar latitude and similar climate and is consistent with a single assemblage for mid-latitudes with similar temperate climate.

4. The distribution of myxomycetes over a continent could occur as assemblages changing gradually, or as a limited number of constant assemblages with abrupt boundaries. This

paper and Wellman (2016), are consistent with the model of there being a limited number of species assemblages, each assemblage being fairly uniform over its extent, and each occurring around the world in areas of similar climate.

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Appendix 1. The location of the survey sites.
+ Sites that include litter-substrate species.

650, 35° 38.29'S, 149° 54.51'E, 766 m.
673, 35° 38.57'S, 148° 59.18'E, 1213 m.
676, 35° 31.06'S, 149° 32.56'E, 1071 m.
677, 35° 25.90'S, 149° 32.30'E, 1125 m.
679, 35° 26.60'S, 149° 32.67'E, 1121 m.
684, 35° 18.49'S, 148° 39.42'E, 1084 m.
715, 33° 53.60'S, 148° 00.23'E, 389 m.
716, 33° 54.42'S, 147° 55.20'E, 277 m.
717, 33° 58.85'S, 147° 59.02'E, 319 m.
719, 36° 10.65'S, 149° 30.94'E, 1086 m.
720, 36° 10.53'S, 149° 31.27'E, 1084 m.
722, 35° 38.79'S, 149° 31.55'E, 1056 m.
723, 35° 38.86'S, 149° 31.75'E, 922 m.
725, 35° 39.86'S, 149° 31.63'E, 914 m.
726, 35° 41.94'S, 149° 32.26'E, 1046 m.
728, 35° 19.82'S, 149° 02.27'E, 580 m.
730, 35° 31.26'S, 149° 34.29'E, 972 m.
731, 35° 30.32'S, 149° 36.08'E, 955 m.
733, 35° 29.93'S, 148° 45.87'E, 1504 m.
741, 35° 30.92'S, 149° 35.02'E, 1003 m.
743, 35° 29.26'S, 149° 37.11'E, 1002 m.
744, 35° 39.67'S, 148° 56.98'E, 1168 m.
745, 35° 39.80'S, 148° 57.03'E, 1142 m.
746, 35 °39.65'S, 148° 57.31'E, 1122 m.
750, 35° 40.15'S, 148° 50.11'E, 1060 m.
751, 35° 40.66'S, 148° 45.02'E, 1420 m.
753, 35° 29.02'S, 148° 53.84'E, 857 m.
754, 35° 29.06'S, 148° 53.81'E, 862 m.
755, 35° 19.82'S, 149° 02.27'E, 580 m.
756, 35° 44.04'S, 148° 29.11'E, 889 m.
757, 35° 43.16'S 148° 29.73'E, 1138 m.
760, 35° 54.69'S, 149° 02.07'E, 1397 m.
761, 35° 29.96'S, 149° 33.60'E, 1095 m.
762, 35° 30.27'S, 149° 32.83'E, 1087 m.
764, 35° 30.20'S, 149° 33.20'E, 1185 m.
767, 35° 41.08'S, 148° 57.92'E, 1152 m.
768, 35° 22.12'S, 148° 49.92'E, 886 m.
784, 35° 29.80'S, 149° 32.93'E, 1160 m.
806, 35° 23.66'S, 148° 49.67'E, 1123 m.
808, 35° 36 08'S, 149° 54.53'E, 816 m.
814, 35° 31.98'S, 149° 33.20'E, 950 m.
815, 35° 31.93'S, 149° 33.19'E, 956 m.
816, 35° 42.20'S, 149° 16.70'E, 1410 m.
818, 35° 23.45'S, 148° 48.45'E, 1264 m.
819, 35° 43.59'S, 148° 30.60'E, 1250 m.
820, 35° 43.97'S, 148° 30.59'E, 1303 m.
821, 35° 44.41'S, 148° 30.93'E, 1329 m.
822, 35° 38.61'S, 148° 26.65'E, 1117 m.
823, 35° 40.50'S, 148° 44.10'E, 1240 m.
824, 35° 40.85'S, 148° 47.69'E, 1523 m.
832, 35° 04.65'S, 150° 24.55'E, 314 m.
842, 35° 27.37'S, 148° 53.23'E, 932 m.
846, 35° 27.34'S, 148° 53.26'E, 937 m.
848, 35° 26.94'S, 148° 53.35'E, 1066 m.
849, 35° 26.84'S, 148° 53.48'E, 1091 m.
850, 35° 45.57'S, 149° 26.74'E, 1070 m.
855, 35° 18.48'S, 148° 39.41'E, 1004 m.
856, 35° 19.07'S, 148° 03.30'E, 856 m.
858, 33° 17.00'S, 149° 05.38'E, 920 m.
857, 35° 20.16'S, 149° 01.47'E, 659 m.
888, 35° 58.90'S, 148° 37.10'E, 450 m.
889, 34° 58.68'S, 148° 37.16'E, 435 m.
891, 35° 59.00'S, 148° 37.00'E, 420 m.
893, 35° 34.25'S, 149° 53.21'E, 834 m.
894, 35° 35.50'S, 149° 45.40'E, 290 m.
897, 37° 06.19'S, 142° 35.36'E, 202 m.
898, 35° 29.71'S, 149° 36.95'E, 975 m.
899, 35° 34.20'S, 149° 57.97'E, 350 m.
901, 35° 28.23'S, 148° 53.32'E, 877 m.
902, 35° 27.36'S, 148° 53.19'E, 928 m.
903, 35° 36.19'S, 150° 19.45'E, 52 m.
904, 35° 33.10'S, 149° 57.11'E, 789 m.
905, 35° 23.32'S, 148° 48.52'E, 1287 m.
906, 35° 23.30'S, 148° 49.90'E, 1000 m.
907, 35° 21.33'S, 148° 50.14'E, 863 m.
908, 35° 21.76'S, 148° 50.30'E, 834 m.
909, 35° 22.12'S, 148° 49.92'E, 888 m.
910, 35° 19.82'S, 149° 02.27'E, 580 m.
911, 35° 19.00'S, 148° 49.00'E, 971 m.
912, 35° 19.23'S, 148° 48.33'E, 1084 m.
913, 35° 19.00'S, 148° 48.26'E, 1138 m.
914, 35° 19.82'S, 148° 48.17'E, 1190 m.
915, 35° 23.32'S, 148° 48.52'E, 1291 m.
916, 35° 08.80'S, 150° 08.50'E, 580 m.
917, 35° 28. 52'S, 149° 34.27'E, 1034 m.
918, 35° 31.93'S, 149° 33.19'E, 956 m.
919+, 35° 21.90'S, 149° 04.00'E, 670 m.
920, 35° 21.99'S, 149° 03.98'E, 693 m.
921, 35° 28.79'S, 149° 34.47'E, 1061 m.
922+, 35° 29.00'S, 149° 33.40'E, 950 m.
923, 34° 57.91'S, 148° 37.80'E, 405 m.
924, 34° 50.48'S, 148° 37.74'E, 380 m.
925, 34° 58.43'S, 148° 37.76'E, 392 m.
926+, 34° 58.12'S, 148° 37.97'E, 383 m.
927+, 35° 16.80'S, 149° 04.70'E, 598
928+, 35° 19.15'S, 149° 04.15'E, 570 m.
929+, 35° 58.00'S, 148° 38.00'E, 440 m.
930+, 35° 16.80'S, 149° 04.70'E, 598 m.
931+, 35° 17.80'S, 149° 04.50'E, 560 m.
932+, 35° 19.20'S, 149° 04.10'E, 570 m.
944, 35 °18.99'S, 148° 48.93'E, 962 m.
941, 35° 18.96'S, 148° 48.83'E, 966 m.
942, 35° 18.97'S, 148° 48.62'E, 996 m.
943, 35° 23.46'S, 148° 49.60'E, 1102 m.
945, 35° 33.74'S, 149° 59.46'E, 196 m.
946, 37° 17.68'S, 149° 44.45'E, 688 m.
947, 37° 12.84'S, 150° 00.79'E, 20 m.
948, 36° 57.28'S, 149° 54.45'E, 16 m.
949, 36° 48.95'S, 149° 56.01'E, 30 m.
950, 37° 01.32'S, 149° 54.47'E, 85 m.
951, 36° 35.58'S, 149° 27.00'E.5
952, 34° 57.60'S, 148° 49.20'E, 440 m.
953, 34° 58.44'S, 148° 37.80'E, 367 m.
954, 34° 58.44'S, 148° 37.80'E, 367 m.
1090, 36° 33.70'S, 150° 02.20'E, 70 m.
1091, 36° 36.30'S, 151° 02.20'E, 10 m.
1092, 35° 58.00'S, 148° 38.00'E, 440 m.

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Patterns of morphological and physiological traits of epiphytes within trees and between elevations in subtropical Australian rainforest

Jennifer C. Sanger & Jamie B. Kirkpatrick

Geography and Spatial Sciences, School of Land and Food, University of Tasmania, Private Bag 78
Hobart Tasmania 7001 AUSTRALIA. Email jennifer.sanger@utas.edu.au

Abstract: Taxonomically dissimilar epiphyte species can have comparable morphological and physiological traits in similar environmental conditions. However, the degree of trait similarity has not been examined in a comparison of bryophytic and vascular epiphytes across elevational and tree gradients. We assess whether epiphyte species that occupy comparable realised niche spaces within host tree and landscape scale gradients have similarities in taxonomy, morphology or physiology. Vascular and moss epiphytes were surveyed within four height zones at five elevations (300-1100 m asl) in the sub-tropical rainforest of Australia. Epiphyte species distributions were agglomeratively classified using Ward's method. Chi square tests were used to test for differences in the incidences of taxonomic groups, life forms, leaf thickness, photosynthetic pathways and other drought resistant morphologies between these distributional groups. These traits were also tested for correlation with light and humidity. Six groups were identified based on distribution. Vascular epiphytes with CAM, thickened leaves and other drought-mitigating morphologies were common in the groups that occupied the most xeric situations. All drought resistant traits were associated with high light and low humidity. Vascular species with few to no drought-mitigating characteristics were common in groups that occupied moister situations. Moss morphology was less congruent with environmental conditions than vascular plant morphology, suggesting that moss life forms are responding to a different scale of environmental variation.

Key words: Drought, Micro-habitat, Morphology, Moss, Vascular epiphytes

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Introduction

Epiphytes use other plants for mechanical support and have no direct connection to the ground, relying on moisture and nutrient inputs from fog and rainfall (Benzing 1990). Hence, epiphytes tend to be more limited by moisture availability than most terrestrial plants (Zotz & Hietz 2001). Lack of water is postulated to be the greatest stress on vascular and bryophytic epiphytes (Zotz & Hietz 2001; Sillett & Antoine 2004; Romanski *et al.* 2011; Bartels & Chen 2012).

Many vascular epiphytes exhibit physiological and morphological characteristics which help them survive drought. Some have Crassulacean Acid Metabolism (CAM) photosynthetic pathways, which help reduce water loss through nocturnal uptake of CO_2 (Winter 1985). Many vascular epiphytes have specialised morphologies that assist with water retention, such as thickened or succulent leaves, or rhizomes and specialised water storage tissue (Hietz & Briones 1998; Benzing 2004; Higgins 2004; Reyes-García *et al.* 2008; Zhang *et al.* 2015).

Epiphytic bryophytes have adapted to drought in different ways to vascular epiphytes. All bryophytes, except one order of hornworts (Anthocerotales), use the C_3 pathway for photosynthesis, a process which is less water efficient than CAM (Smith & Winter 1996; Raven *et al.* 1998; Hanson & Rice 2013). Instead, bryophytes, and some pteridophyte species (such as resurrection plants), are poikilohydric, in that they can rehydrate upon wetting from a desiccated state (Proctor 1990; Bates 1998; Sillett & Antoine 2004). Bryophytes also have a range of forms, which can assist in water storage (ver Leerdam *et al.* 1990; Hedenäs 2001; Frahm 2003; Sillett & Antoine 2004). For example, bryophytes that form dense mats can store water in the capillary spaces between the leaves (Bates 1998; Frahm 2003; Sporn *et al.* 2010).

Within the host tree, light, temperature, wind, and moisture vary from the moist, shaded base of the trunk to the more arid and exposed outer branches (Wallace 1981; Théry 2001; Bartels & Chen 2012). Distinct patterns in the distributions of morphological and physiological traits of epiphytes occur within the host tree (Pittendrigh 1948; Johansson 1974; Hietz & Briones 1998; Reyes-Garcia *et al.* 2012). Vascular epiphytes inhabiting the shadier and more humid lower zones of the tree tend to have fewer traits associated with drought resistance, while species with traits such as CAM, succulence, thickened and smaller leaves are common in the sun-exposed outer crown (Johansson 1974; Winter *et al.* 1983; Hietz & Briones 1998). Bryophytes adapted to water storage, such as mats, occur in the exposed parts of the canopy, while light-gathering bryophytes, such as dendroids (fan shaped mosses), are more common in the shady bases of host trees (Bates 1998; Acebey *et al.* 2003; Silva & Porto 2013).

At the landscape scale, moisture and temperature vary with elevation, and montane environments are frequently shrouded in cloud, resulting in high levels of humidity and rainfall (Chantanaorrapint 2010; Strong *et al.* 2011; Ding *et al.* 2016). There are distinct distributions of morphological traits in both epiphytic and terrestrial ferns with elevation in Hawaii, with more divided fronds at higher elevation (a function to collect more moisture from fog), longer blades in shaded habitats, and fronds with shorter stipes and fewer pinnae in drier habitats (Creese *et al.* 2011). Macro-lichens have a high level of branchiness at higher elevations, which is inferred to be a response to high levels of fog, as increased branchiness assists with fog interception (Stanton & Horn 2013). Many studies which describe the distributions of epiphyte morphologies and physiologies are restricted to within the host tree. There are few that cover landscape gradients (e.g. Mantovani 1999) and none that cover both gradients.

There are approximately 400 epiphyte species in Australia (Wallace 1981) and they are a prominent feature in rainforests, yet few comprehensive epiphyte studies have been conducted. In recent years, the distribution of Australia's epiphyte species have been examined over host tree and elevation gradients (Sanger & Kirkpatrick 2015, 2017). Other studies on the ecology of Australia's vascular epiphytes are limited to a few studies (Wallace 1981; Cummings *et al.* 2006; Freiberg and Turton 2007), as are studies on epiphytic bryophytes (Fensham and Streimann 1997; Franks and Bergstrom 2000; Ramsay and Cairns 2004). With one exception (Sanger & Kirkpatrick 2015), studies of epiphytic bryophytes in tropical and subtropical rainforest in Australia have been limited to the lower trunk of the host.

In the present study, we assess which vascular and moss epiphytes share similar niche spaces within the host tree and across elevational zones in the subtropical rainforests of Australia. We determine whether species with morphological and physiological similarities are found in the same habitats. We expect that species that are common in more xeric situations will have morphologies and physiologies that assist with drought resistance. Finally, we determine whether there are differences between mosses and vascular plants in the strength of the relationship between morphology and environment.

Methods

Study Area

The study was conducted in the Border Ranges National Park (28°21′35″S, 152°59′10″E), a World Heritage-listed subtropical rainforest that covers 3,600 km^2 in northern New South Wales, Australia. A set of long term monitoring plots, along a transect ranging from 300 to 1100 m in elevation, with plots at 200 m intervals, is located on the western side of the Border Ranges National Park (Kitching *et al.* 2011). Further details of the study site and general patterns of epiphyte distribution on this transect can be found in Sanger & Kirkpatrick (2015).

There are limited climate data (temperature only) available for the Border Ranges; however, more detailed climate information exists for a transect of similar design at Lamington National Park, which is located 20 km from the Border Ranges transect in the same mountain range. Temperature measurements for the two transects indicate a similar environmental lapse rate for median temperatures (Fig. 1; Maunsell *et al.* 2015). At Lamington, temperature and humidity data loggers were installed in the canopy and understory (Strong *et al.* 2011). The average annual temperature decreased by 0.75 °C with every 100 m gain in elevation, equating to a difference of 6-7 °C between 300 and 1100 m (Strong *et al.* 2011). During the dry season (August and September), relative humidity at midday increased linearly from the 300 m site (canopy: 25%; understorey: 45%) to the 1100 m site (canopy: 60%; understorey: 80%; Strong *et al.* 2011). There was little difference in humidity during the wet season (February and March), with humidity levels at close to 100 percent within the canopy and understory at most elevations (Strong *et al.* 2011). Any climatic differences between the Lamington and Border Ranges areas are likely to be small, as the hot drying weather comes from the northwest, and the two areas from which data were collected are north-facing (Lamington) and west-facing (Border Ranges) and have similar altitudinal vegetation zonation patterns.

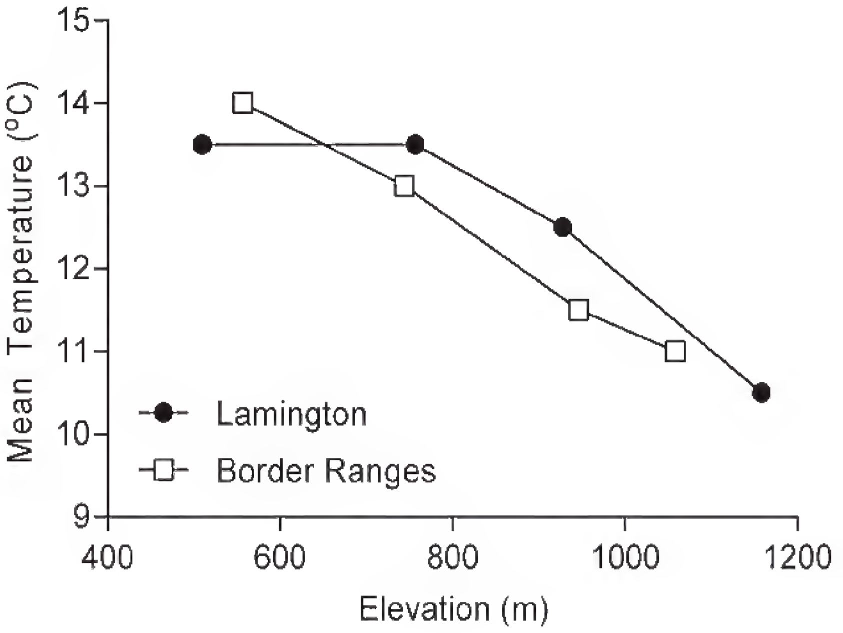

Fig. 1: Median temperatures calculated from data loggers, which recorded temperature every 3 h from July 2012 to Feb 2013 and April to July 2013 (data from Maunsell *et al.* 2015). The lowest elevation Lamington site is subject to cold air drainage.

Epiphyte sampling

We collected our data between May and July 2013. Within each of the five elevations, ten suitable large trees closest to the centre of the plot were selected. Trees were selected for their suitability for climbing (healthy trees with no obvious signs of rot, with large sturdy branches within 30 m of the ground, unobstructed by large woody vines). Approximately a quarter of trees within the plots had large woody vines in the inner canopy. These vines can alter the microclimate and may negatively affect the abundance of epiphytes. We chose not to climb trees with large woody vines, because of their lack of safety, and we acknowledge that this choice may have affected our results. Trees were climbed using a combination of single and double rope techniques (Lowman & Moffett 1993). The species, height, tree diameter at breast height (DBH - measured at a height of 1.3 m), and the elevation and GPS location were recorded for each host tree. Fifteen tree species from ten families were sampled (see Table 2.1). Average tree diameter at breast height was 54.5 ± 15 cm at 300 m, 66.6 ± 16 cm at 500 m, 62 ± 19 cm at 700 m, 50.2 ± 15 900 m and 72.2 ± 32 m at 1100 m.

Each tree was divided into height zones, adapted from the zonation system used by Johansson (1974). Following ter Steege & Cornelissen (1989), Romanski *et al.* (2011) and Gehrig-Downie *et al.* (2011), we divided the trunk into two zones, as the upper trunk often had a very different microclimate to the lower trunk. Four height zones were surveyed: inner canopy (the inner third of the branches in the crown), the upper trunk (the mid-point of the trunk to the first bifurcation), the lower trunk (two metres above the base of the trunk to the mid-point of the trunk), and the base (from the ground to 2 m). The outer and mid-canopy were not surveyed as these zones are often difficult to access safely. In each height zone of each tree, the number of individuals of each species of vascular epiphytes was recorded. Clumped or rhizomatous plants were counted as one individual, following Sanford (1967). Specimens that could not be identified in the field were collected and taken to the Queensland Herbarium (BRI) for identification.

We wished to produce a list of moss taxa for each zone on each tree. Due to the patchiness of bryophytes within the host trees, randomly place quadrats (Gradstein *et al.* 1996) were not used, as richness would have been underestimated. Following Wolf (1993), subsamples were collected from different microenvironments within the zone or wherever there appeared to be a distinct change in bryophyte species composition. Ten to 15 subsamples were normally collected from each zone. Samples were taken to the Queensland Herbarium for sorting into morphospecies and identified to either genus or species level where possible. No cover estimates or abundance data were recorded. We focused on mosses to reduce the likelihood of missing rare or inconspicuous cryptogam species. Nomenclature for both vascular and non-vascular species follows the Catalogue of Life (Roskov *et al.* 2015). Herbarium vouchers were deposited in the Queensland Herbarium, Brisbane.

The life form of each epiphyte was noted. Vascular epiphytes were placed into one of three categories: holo-epiphytes, primary hemi-epiphytes and nomadic vines. Holo-epiphytes spend their entire life cycle on the host tree without connection to the ground or the vascular system of the host (Kelly 1985; Benzing 1990). Primary hemi-epiphytes are plants that begin their life cycle as true epiphytes but later send feeder roots down the trunk of the host tree and connect to the ground (Kress 1986; Benzing 1990). Nomadic vines (also known as secondary hemi-epiphytes), such as species belonging to the genera *Phymatosorus*, *Arthropteris* and *Pothos*, are semi-epiphytic climbers which are functionally similar to epiphytes, as their adventitious roots are often used for nutrient and water uptake and they occasionally lose their connection to the ground (Wallace 1981; Moffett 2000; Zotz 2013). Five types of moss life form were identified: dendroid, pendant, mat, tuft and weft, based on Bates (1998), Kürschner *et al.* (1999) and Frahm (2003).

For each epiphyte species, leaf thickness was measured on specimens collected in the field and also reconfirmed from herbarium vouchers at the Queensland Herbarium. Due to the difficulties with examining the thickness of the dried leaves of specimens, species were divided into two leaf thickness classes: thick (≥ 1 mm) and thin (< 1 mm). Features such as glossy, leathery or reduced leaves, pseudobulbs, and the presence of detritus-collecting baskets were also recorded for each species as 'other drought morphologies', as determined from field observations and from Wilson (1990) and Bernhardt (1993). Glossy and leathery help prevent water loss due to a thicker cuticle and reduced leaves prevent water loss due to a decrease in surface area (Benzing 2004, Higgins 2004). Detritus-collecting baskets are able to store water in the soil and hummus collected in the basket (Wallace 1981). The presence of CAM in vascular species or the presence of poikilohydry in mosses and some fern species was noted. For the vascular species, the presence of CAM or C_3 pathways followed Winter *et al*. (1983), who assessed the CAM status of 157 vascular epiphytes from Australia by examining the stable carbon isotope ratio ($\delta^{13}C$) values and the absence of Kranz anatomy. Species are said to have CAM pathway if $\delta^{13}C$ values were less than -20 ‰. Twelve species found in the current study were not assessed by Winter *et al.* (1983), with most of these species being nomadic vines. All moss species are known to use the C_3 pathway (Smith & Winter 1996; Raven *et al.* 1998; Hanson & Rice 2013).

Light was estimated using hemispherical canopy photography. This is a widely used method to calculate total transmitted light for a particular point (Frazer *et al.* 1999). A Cannon 5D mark III digital camera (Ohta-ku, Tokyo, Japan) with a Rokinon 8mm f/3.5 HD Fisheye Lens (Gangnamgu, Seoul, Korea) was used to take three to five hemispherical photos within each height zone, on both the north and south side of each tree. It is recommended to take photos on uniformly overcast conditions in order to remove the effect of direct solar irradiance; however, due to our limited time in the field, this was unachievable. Instead, to control for direct solar irradiance, all photos were taken in manual mode with adjusted shutter speed and aperture to best suit light conditions. To standardize the photos and to reduce highlights from around the edge of leaves, light levels were balanced using a standardised histogram reference in Photoshop (Adobe, San Jose, CA, USA). Photos were then analysed using Gap Light Analyser (Frazer *et al.* 1999) which calculates the percentage of total transmitted light for each image over an entire year by transforming the image pixel positions into angular coordinates (Frazer *et al.* 1999).

Data analysis

The presence/absence of each vascular and moss species was noted for each height zone for each tree surveyed. The data were then summed across the ten tree replicates at each site to create a frequency of species occurrence within each of four height zones over each of the five elevations (n = 20). Ward's technique for agglomerative cluster analysis (Ward 1963) was used on a Euclidean distance matrix to identify groups of species with similar distributions in the 20 elevation by tree zone samples. These groups were plotted in three dimensions (stress = 0.14) using global non-metric multidimensional scaling (MDS) with Bray-Curtis distance values, 25 iterations and a 0.1 (10%) stress stopping rule.

Chi square was used to test whether the numbers of species in each of the distributional groups differed from the rest of the species at $p < 0.05$ in photosynthetic pathway (CAM and C_3), leaf thickness (thin and thick), life form (holoepiphyte, nomadic vine, dendroid, pendant, mat, tuft and weft), the presence of other drought morphologies (pseudobulbs, leathery leaves, glossy leaves, basket forming) or taxonomic group (vascular and mosses). The expected values were calculated from the proportions of the types within the species list as a whole. Rank order correlation was used to assess whether the above mentioned traits were related to humidity and/or light. The percentage of species with a particular trait was calculated for each zone/elevation and was rank order correlated with the humidity and light averages for each zone/elevation. Classification and correlation tests were performed using Minitab 16.1.0 (MINITAB, Pennsylvania, USA). MDS plots were created using Primer v.6 with PERMANOVA+ add-on software (Primer-E Ltd, Plymouth, UK).

Results

Thirty-four species of vascular epiphytes (17 species of pteridophytes, 13 species of Orchidaceae and four species of Dicotyledonae) and 42 morphospecies of moss were recorded. There were six distinct distributional groups of species (Figs. 2, 3, 4). The species in Group 1 occupied some of the more humid locations, as they inhabited the lower tree height zones and had a broad distribution over the elevation gradient (Fig. 3). The species in Group 2 occurred in the more xeric ends of the two gradients: the upper height zones and lower elevations (Fig. 3). Group 3 consisted of species that had distributions over the mid to upper height zones and were distributed mainly around the mid elevations (Fig. 3). Group 4 had species which occurred in the upper height zones and the high elevations (Fig. 3). Group 5 contained species that were concentrated in the higher elevations and occurred over the entire tree height gradient (Fig. 3), thus, were mostly in humid environments (Table 1). Group 6 contained species that occurred in the upper height zones across all elevations (Fig. 3). Each group occupied a largely distinct part of ordination space (Fig. 4).

Group 6 had more pteridophyte species ($Chi^2 = 7.06$; df = 1; P = 0.008) and fewer mosses ($Chi^2 = 4.40$; df = 1; P = 0.034) than would be expected by chance (Table 1). Group 2 had a significantly higher proportion of orchids than the rest ($Chi^2 = 7.86$; df = 1; P = 0.005). Groups 1, 2 and 4 had an even mix of mosses and vascular species, while groups 3 and 5 were dominated by mosses. The five species of nomadic vine all belonged to Group 1 ($Chi^2 = 10.16$; df = 1; P = 0.001). Six of the nine species in group 5 were tuft mosses ($Chi^2 = 11.39$; df = 1; P < 0.001). There were a higher proportion of holo-epiphytes in groups 6 than expected by chance ($Chi^2 = 11.39$; df = 1; P < 0.001).

Table 1: The percentage of species in each group with particular attributes. Int = intermediate moistness.

Group	1	2	3	4	5	6
Moistness	***Humid***	***Dry***	***Int***	***Int***	***Humid***	***Int***
Taxonomic						
Moss	19	14.3	19	26.2	16.7	4.8
Vascular	17.6	32.4	5.9	14.7	5.9	23.5
Life form						
Mat	25	33.3	16.7	25	0	0
Weft	33.3	0	33.3	33.3	0	0
Tuft	0	0	0	7.7	46.2	46.2
Dendroid	40	10	20	0	10	20
Pendant	0	25	50	25	0	0
Nomadic vine	100	0	0	0	0	0
Holo-epiphyte	0	40	8	16	4	32
Primary hemi-epiphyte	0	100	0	0	0	0
Filmy Fern	33.3	0	0	33.3	33.3	0
Photosynthetic pathway						
C_3	15.8	14	15.8	22.8	14	17.5
CAM	0	66.7	11.1	11.1	0	11.1
Unknown	30.8	30.8	23.1	7.7	7.7	0
Leaf thickness						
Thin	22.6	16.1	14.5	22.6	14.5	9.7
Thick	0	50	7.1	21.4	0	21.4
Other morphology						
Basket-forming	0	66.7	0	0	0	33.3
Leathery leaves	55.6	0	11.1	22.2	0	11.1
Pseudobulb	0	28.6	28.6	28.6	0	14.3
Glossy leaves	0	25	0	0	0	75
Reduced leaves	0	100	0	0	0	0

Table 2: The correlation of attributes with humidity and light. Spearman's rank order correlation co-efficient (r) and p values are shown. Significant p values are shown in bold.

	Humidity		**Light**	
Attribute	*r*	*p-value*	*r*	*p-value*
Taxonomic				
Moss	-0.021	0.928	0.139	0.558
Vascular	-0.441	0.051	0.48	0.032
Life form				
Dendroid	0.282	0.229	-0.448	**0.048**
Filmy fern	0.145	0.541	-0.088	0.712
Holo-epiphyte	-0.658	**0.002**	0.745	**< 0.001**
Mat	-0.059	0.805	-0.078	0.743
Nomadic vine	0.769	**< 0.001**	-0.65	**0.002**
Pendant	-0.859	**< 0.001**	0.596	**0.006**
Tuft	0.228	0.333	0.417	0.067
Weft	0.689	**0.001**	-0.621	**0.003**
Photosynthetic pathway				
CAM	-0.75	**< 0.001**	0.693	**0.001**
C_3	-0.122	0.609	0.252	0.284
Leaf thickness				
Thick leaves	-0.725	**< 0.001**	0.778	**< 0.001**
thin leaves	-0.113	0.634	0.152	0.523
Other morphology				
Basket forming	-0.646	**0.002**	0.642	**0.002**
Pseudobulb	-0.583	**0.007**	0.599	**0.005**
Leathery leaves	-0.76	**< 0.001**	0.773	**< 0.001**
Glossy leaves	-0.544	**0.013**	0.633	**0.003**

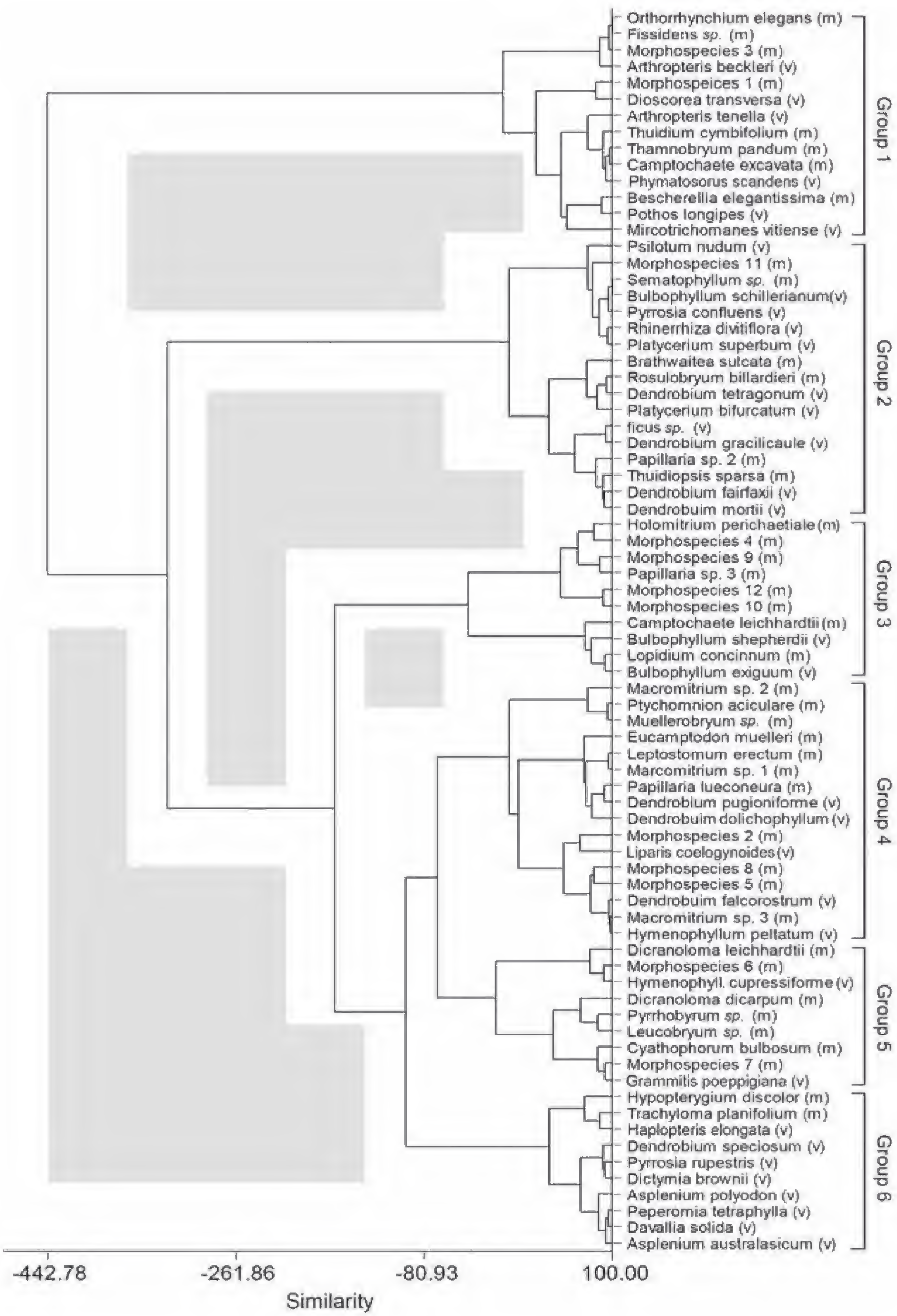

Fig. 2: Dendrogram showing the six groups of vascular (v) and moss (m) species with similar distributions over the two gradients: tree height and elevation.

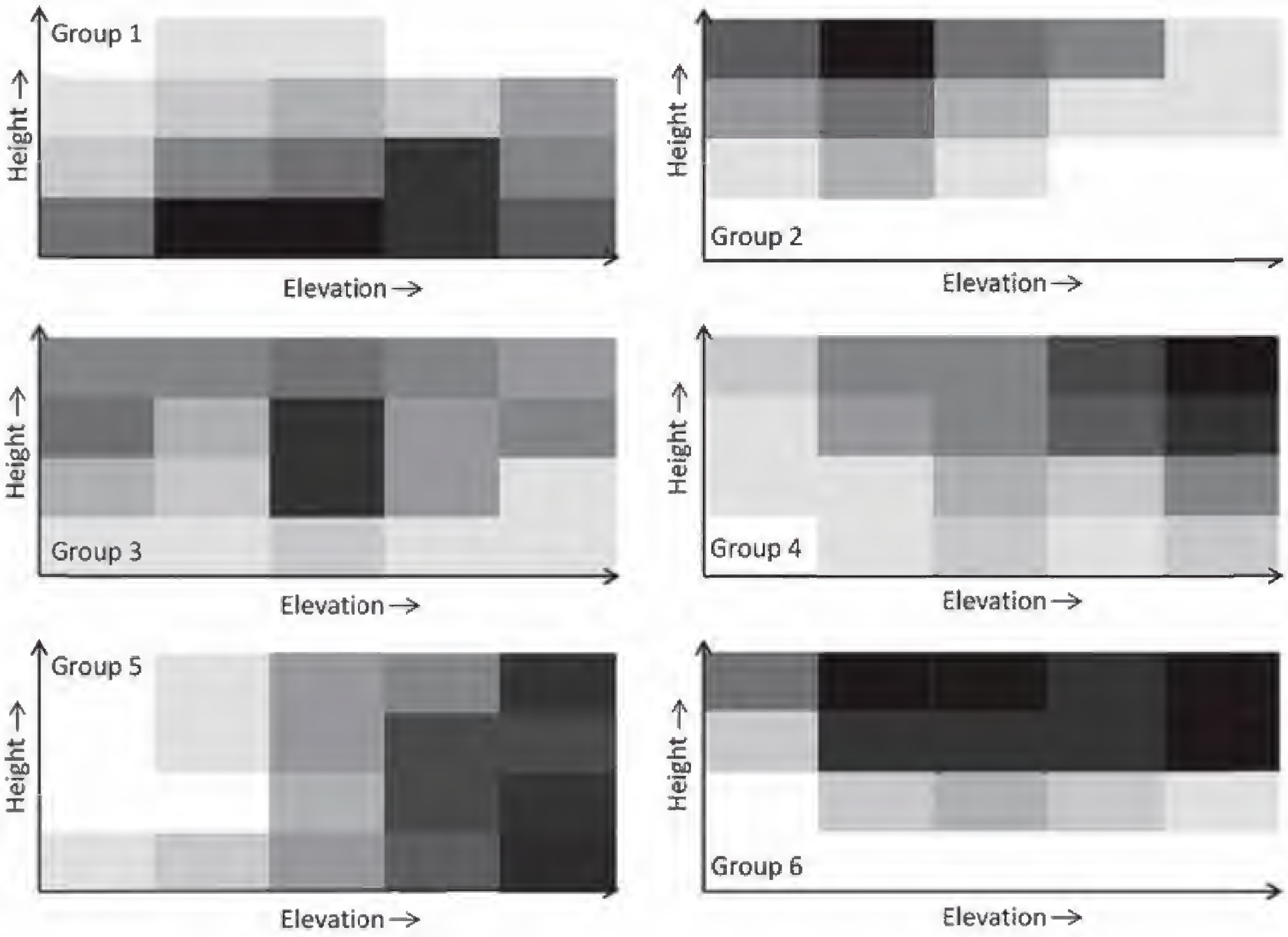

Fig. 3: The epiphyte species richness over the height and elevation gradients for each group. Shading represents the number of species in each height zone / elevation, with the lightest shade of grey representing one species and black representing all species in the group.

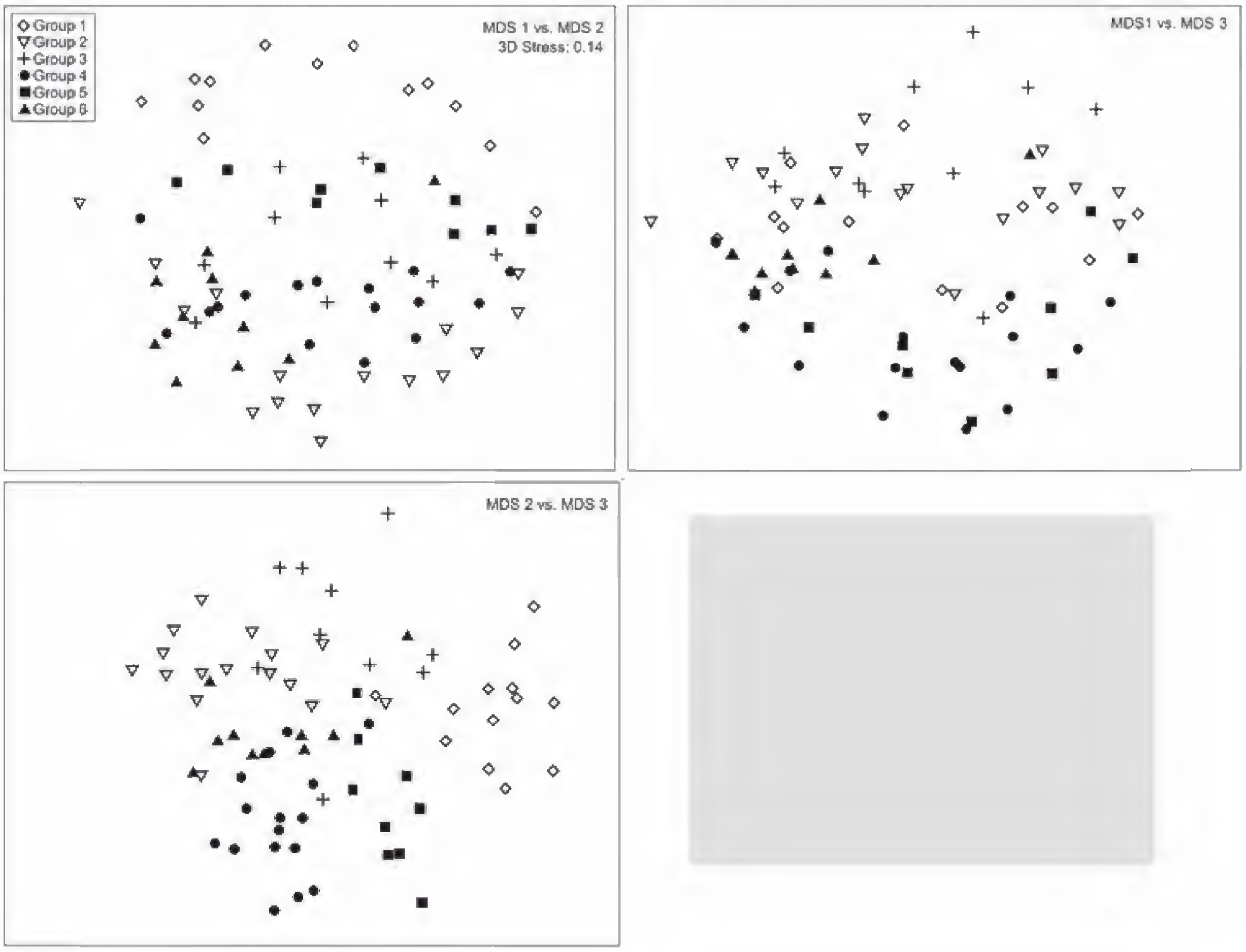

Fig. 4: MDS plots depicting the distributions of epiphyte species in the six groups.

Group 2 had a significantly higher proportion of known CAM species than the rest ($Chi^2 = 5.45$; df = 1; P = 0.02). All other groups either had no species exhibiting CAM (groups 1 and 5) or contained only one or two CAM species (groups 3, 4 and 6). For leaf thickness, only group 2 had a significantly higher proportion of thick leaved species ($Chi^2 = 5.72$; df = 1; P = 0.02). Groups 1 and 5 only contained species with thin leaves. Species in Group 2 ($Chi^2 = 9.24$; df = 1; P = 0.002) and Group 6 ($Chi^2 = 4.31$; df = 1; P = 0.04) had a higher proportion of species with other drought resistant morphologies, while Group 1 ($Chi^2 = 5.58$; df = 1; P = 0.02) and Group 5 ($Chi^2 = 5.38$; df = 1; P = 0.02) contained no species with other drought-mitigating morphologies (Table 1).

CAM, thick leaves, leathery leaves, glossy leaves and pseudobulbs were positively correlated with light and negatively correlated with humidity, as were the holo-epiphyte, basket forming, and pendants lifeforms (Table 2). Nomadic vines and the weft life form showed the opposite pattern, with a negative correlation with light and a positive correlation with humidity (Table 2). Vascular epiphytes were positively correlated with light and the dendroid life form was negatively correlated with light (Table 2).

Discussion

There was a strong correlation of drought-resistant traits in high light, low humidity conditions. Furthermore, species with these traits were most commonly located in the upper tree zones and lower elevations, where conditions are generally drier. The group (2) that occupied the driest habitats had a high concentration of species with CAM, an adaptation possessed by approximately two-thirds of Australia's orchid species (Winter *et al.* 1983; Holtum & Winter 1999). *Pyrrosia confluens*, one of the few Australian pteridophyte species to exhibit CAM (Winter *et al.* 1983) was also in the group. The occupation of the driest and most exposed habitats by CAM epiphyte species is widespread, having been noted in lowland forest in Panama (Zotz & Ziegler 1997), Trinidad (Griffiths & Smith 1983) and in Australia (Winter *et al.* 1983). CAM has also been found to be more prevalent in vascular epiphytes at low elevations where climatic conditions are drier (Earnshaw *et al.* 1987; Silvera *et al.* 2009).

In addition to a high concentration of species with CAM, this dry habitat group had a high proportion of species with thick leaves, a trait which was also found to be correlated with low humidity and high light conditions. Thickened leaves assist in water retention and are commonly associated with dry microsites (Pittendrigh 1948; Johansson 1974; Hietz & Briones 1998; Mantovani 1999). Other drought-mitigating features had a strong correlation with low humidity and high levels of light, and a high proportion of species with these traits were present in Group 2. For example, *Platycerium bifurcatum* and *Platycerium superbum* are nest-forming pteridophytes which accumulate litter and dead fronds that assist in retaining moisture around the roots (Wallace 1981). *Platycerium bifurcatum* also has specialised water-storage tissue (Kreier & Schneider 2006) and the epidermis of the sporotrophophyll leaves are covered by hairs which decrease water loss (Rut *et al.* 2008). The orchids in Group 2 possessed other morphological characteristics that would help them resist drought, such as specialised root systems and pseudobulbs (Benzing 2004; Higgins 2004).

The majority of the vascular species that had no obvious characteristics to cope with drought occurred in groups distributed over the more humid ends of the two gradients, a pattern which has been observed elsewhere (Johansson 1974; Hietz & Briones 1998). In Groups 1 and 5, which were concentrated at high elevations or in the lower zones of the tree, thin leaves, C_3 pathway, and a lack of apparent morphological adaptations to drought were almost ubiquitous. The ordination of species further highlights the distribution of the groups over the moisture gradient, with Groups 1 and 2 being the most separate in ordination space.

Some of the vascular epiphytes in the groups that occupied sites with deduced intermediate moisture levels exhibited apparent drought adaptations. The species in Group 6 were likely to be subject to some drought stress, as they were restricted to the upper height zones. While there was not a significantly higher proportion of either CAM or thickened leaves in this group, there were a high proportion of other apparent drought adaptations. This group was dominated by pteridophytes, which generally occupy wetter habitats than orchids (Wallace 1983; Benzing 2004) and have features such as leathery or glossy leaves or basket formations.

As expected, mosses were dominant in groups which were distributed in the mid to upper elevations, where humidity is high and temperatures are mild (Wolf 1994; Benzing 1998; Sillett & Antoine 2004). However, there were also moss species present in the group which occupied the driest habitat, a pattern which highlights the wide ecological range of mosses (Holz *et al.* 2002; Acebey *et al.* 2003; Romanski *et al.* 2011; Silva & Pôrto 2013). While we found clear distribution patterns in the morphology and physiology of vascular species related to moisture, not all of the moss life forms conformed to the pattern expected from the literature. Only dendroids and wefts, which were correlated with low light conditions, were closely consistent with previous observations. These life forms have been described as adaptions to gather more light (Frahm 2003; Sporn *et al.* 2010). The pendant life form is usually found at higher elevations where their narrow feathery stems can facilitate the uptake of atmospheric water (Bates 1998; Kürschner *et al.* 1999; Romero 1999; Frahm 2003; Parolly & Kürschner 2004); however, this life form was found in the most xeric sites and was correlated with low humidity. Tufts were concentrated in the high elevation group (Group 5) where humidity levels are generally higher, which is consistent with previous research (Frahm 2003), yet this life form had no significant correlation with humidity. Additionally, mats occurred in shady and moist environments; however, this life form is very effective at storing water in the capillary spaces created between the individuals, making them characteristic of light-intensive, dry microclimates (Bates 1998; Acebey *et al.* 2003; Frahm 2003).

We hypothesise that this seemingly poor fit between moss morphology and microclimate, compared to that of the vascular species, may be a reflection of differences in scale of occupancy between the two taxonomic groups. For example, mosses, being much smaller than the vascular species, may be able to occupy tiny areas of moisture within dry habitats, like the shady undersides of branches or small fissures in the bark, whereas the size of vascular plants might preclude such occurrence. Vascular species could also alter the microclimate of patches of the inner canopy by creating shade, which could easily be exploited by smaller organisms, such as mosses. A test of the above hypotheses would require detailed mapping of species distributions and microhabitats on trees, rather than the broad zonal approach we have adopted.

We acknowledge that there are some limitations in using physiology and morphology data from other studies. For instance, other methods to test for CAM or testing species under drought conditions may yield different results to that reported by Winter *et al*. (1983). Two basket fern species present in the group occupying the most xeric habitat, *Platycerium bifurcatum* and *Platycerium superbum*, were not identified as having a CAM when tested under non-drought conditions using carbon isotope ratios (Winter *et al*. 1983). However, CAM is often more easily detected in drought-stressed individuals (Cushman & Borland 2002; Rut *et al*. 2008). Subsequent studies measuring CAM in *Platycerium bifurcatum* under drought conditions have found that CAM was present in the cover leaves (Rut *et al*. 2008). Weak CAM has also been found in closely related *Platycerium veitchii* by testing for nocturnal increases in titratable acidity rather than using carbon isotope ratios (Holtum & Winter 1999).

By using objective classification of species groups and by testing the correlation of drought resistance features with light and humidity, we have reinforced the generalisation that vascular epiphyte species have sets of morphological and physiological characteristics that are congruent with within tree and elevational variation in environment, which represents strong gradients in moisture and humidity. We found that, at our scale of inquiry, many moss species had morphological characteristics that appeared inappropriate for the environments occupied by their group. This has led us to propose the hypothesis that they were responding to a different scale of habitat variation than the zone. There is a need to focus on the distribution of mosses at this finer scale and to determine how climatic change is likely to impact on future distributions of these cryptic species.

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Is there a relationship between contemporary high Aboriginal plant resource locations and mapped vegetation communities?

J.T. Hunter

School of Environmental and Rural Science, University of New England, Armidale, NSW 2350 AUSTRALIA

Abstract: Across western New South Wales agricultural practices have led to significant changes in the distribution and abundance of many native plant species. These changes have occurred due to past clearing practices and the introduction of grazing and pest animals. It is likely that such changes have affected the distribution of plant species used by Aboriginal peoples, and that formerly rich plant resource areas may also have changed. Here an attempt is made to map contemporary high aboriginal plant resource areas in the Yantabulla area (lat 29° 55'S, long 150° 37'E) of far western New South Wales, using kriging interpolation. High aboriginal plant usage resource areas were not found to be correlated with any particular vegetation assemblage, although Lignum Shrublands comparatively had the lowest scores. Site species richness was correlated strongly with sites of high abundance of aboriginal resource use. It is hoped that by identifying contemporary high resource locations, new understandings of the landscape can be developed by traditional owners and conservation land managers.

Keywords: kriging interpolation, food, medicine, tools, ceremonial.

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Introduction

As with all human cultures Aboriginal peoples are likely to have caused vegetation modifications at various scales including encouraging mosaics and edge areas, resetting successional sequences, creating wild stands and informal 'orchards' (by favouring perennial fruit, nut and tuber bearing species) and increasing the prevalence of prey abundance in specific locations (Smith 2011). These may have been achieved passively or more directly by the use of fire (Latz 1995; Vigilante & Bowman 2004; Smith 2011). However in most current Australian landscapes, what minor or major modifications may have occurred due to Aboriginal influence over millennia, have been greatly modified by the more intensive post-settlement European farming practices. In spite of this, it is likely that the natural distribution of many species important to Aboriginal peoples will have maintained their general distribution across the landscape, as their occurrence is based on features of climate and soil (Gaikwad *et al.* 2011).

Plants used by Aboriginal peoples are culturally valuable but knowledge of high resource areas is inadequate and fragmented. This is particularly so since much traditional knowledge is now lost. Major changes in landscape management have changed patterns that may have been prevalent in the past causing redistribution, losses and increases in abundance of many plant species through large areas being cleared, changed fire regimes and more intensive primary production. In western NSW many plant communities now have extensive woody encroachment and are now dominated by native species thought to have increased in distribution since clearing and grazing were introduced (Eldridge *et al.* 2013). Such taxa include *Dodonaea viscosa* and *Eremophila sturtii* which are often termed 'woody weeds' (Porteners *et al.* 1997). Additionally, a number of dominant and characteristic species in western NSW and across the semi-arid regions of Australia (e.g. *Acacia aneura, Acacia oswaldii, Alectryon oleifolius, Atalaya hemiglauca, Casuarina pauper, Flindersia maculata, Grevillea striata, Hakea ivoryi, Hakea tephrosperma, Hakea leucoptera & Ventilago viminalis*), which appear to recruit via seed only infrequently, may not have returned to their original abundances post-clearing (Batty & Parsons 1992; Auld & Denham 2001). This is probably due to a number of these taxa having evolved in the arid and semi-arid regions of Australia (in the Cretaceous-Palaeocene when the climate was warmer, and more seasonal) (Specht & Specht 1999). Unpredictable rainfall, lack of seasonality and increasing aridity over millennia followed; these conditions are likely to be further exacerbated by predicted anthropogenic climate change further reducing the likelihood of future seeding recruitment in these species (CSIRO & Bureau of Meteorology 2015).

Adjoining properties *Naree* and *Yantabulla* in far western NSW are associated with Cuttaburra Creek, which flows into Yantabulla Swamp, and eventually into the Paroo River. *Naree* Station (15,000 ha) a former pastoral property was purchased by Bush Heritage Australia in 2012 (http://www.bushheritage.org.au/places-we-protect/new-south-wales/naree). In 2015 the southern neighbouring pastoral property of *Yantabulla* Station (16,000 ha) was purchased by South Endeavour Trust (http://www.southendeavour.com.au/). Both properties are currently managed for wildlife conservation by Bush Heritage Australia. Until the recent changes in ownership and their subsequent emphasis on conservation management, these properties were under grazing management for more than 100 years. The properties contain a range of landscapes including extensive ephemeral wetlands (billabongs, riverine lakes, terminal lakes), floodplains, dunal areas and low lying escarpments. These systems are dominated by a variety of broad vegetation assemblages including: Coolibah, Poplar Box and Blackbox Woodlands; shrublands of Mulga, Ironbwood, Lepardwood, Belah, Rosewood, Turpentine and Hop Bush; Grasslands; Canegrass and Lignum (Hunter & Hunter 2016).

The traditional owners of the lands covering these stations are the Budjiti people, and Bush Heritage Australia aims to work with, and strengthen the relationship with traditional owners and to create opportunities to involve them in identifying and protecting cultural values (http://www.bushheritage.org.au/places-we-protect/new-south-wales/naree). As we may not know the nuances of native plant species distributions and their abundances in pre-European times, investigations have to rely on current distributions and abundances. In this paper we attempt to map areas of high and low plant resources that may have been used by Aboriginal peoples at *Naree* and *Yantabulla*, to assist planning for the protection of potential culturally important areas. We use the data to test if there is congruence between defined vegetation units and areas generally high in species richness.

Methods

Naree and *Yantabulla* stations (31 990 ha in area) are 60 km south east of Hungerford and 112 km north-west of Bourke (lat 29° 55'S, long 150° 37'S) on Cuttaburra Creek within the Mulga Lands Bioregion (Thackway & Cresswell 1995). Here a total of 208 full floristic 20 x 20 m sites were surveyed for vascular plants. Sites were surveyed during June 2014 and April 2015, and all sites revisited in April 2016. All vascular plant species were scored using a modified cover abundance scale (scores: 1: <5% and uncommon; 2: <5% and common; 3: 6-20%; 4: 21-50%; 5: 51-75%; 6: 76-100%) (Westhoff & Maarel 1978). These scores were converted to the medial score for each cover category in order to redress the emphasis on low cover scores. Site scores were then divided by the lowest site score obtained for standardisation. Nomenclature follows PlantNET (http://plantnet.rbgsyd.nsw.gov.au/), accessed January 2016.

Taxon-related tables were created that included information on species score within each plot and a table of traits associated with Aboriginal usage for each species (Maiden 1889; Henshall *et al.* 1980; Cunningham *et al.* 1981; Levitt 1981; Cribb & Cribb 1982; Leiper & Houser 1984; Goddard & Kalotas 1985; Low 1985; Cribb & Cribb 1986; Low 1988; Low 1989; Low 1990; Wightman & Smith 1989; Smith & Wightman 1990; Wightman *et al.* 1991; Wightman *et al.*

1992ab; Zola & Gott 1992; Lazarides & Hince 1993; Leiper & Houser 1993; Latz 1995; Bindon 1996; Stewart & Percival 1997; Maslin *et al.* 1998; Harris *et al.* 2000; Lassack & McCarthy 2011; McKerney & White 2011; Williams 2011) (Appendix 1). Trait use of all species were weighted by their score from each plot. Kriging interpolation was used on site based plant usage scores to model the density of aboriginal plant usage across *Naree* and *Yantabulla* stations using Surfer (Vers. 14.3.691; Golden Software). Kriging is a very flexible geostatistical gridding method that produces maps from irregularly spaced data by allowing custom-fit to data by specifying the appropriate variogram model and incorporating anisotropy and underlying trends.

Hunter and Hunter (2016) used this same floristic data to produce a phytosociological classification and vegetation map within a three-tiered system based on the EcoVeg criteria (Faber-Langedoen *et al.* 2014) (Group, Alliance and Association). The Group and Alliance levels of floristic classification are used here for analysis (Table 1). The Canegrass Alliance of Hunter & Hunter (2016) has not been used as only two sites were surveyed in this assemblage which would not allow for statistical inferences to be made.

Table 1: Hierarchical floristic classification units of Group and associated Alliances within the study region (Hunter and Hunter 2016).

Floristic Group	Floristic Alliance
Mulga Complex	A. Mulga Shrubland
Shrubland Complex	B. Turpentine – Button Grass – Windmill Grass Shrubland
	C. Turpentine – Hop Bush – Kerosene Grass Shrubland
Floodplain Wetlands Complex	D. Coolibah – Black Box – Yapunyah – Lignum Woodlands
	E. Rat's-tail Couch – Love Grass Grasslands
	F. Canegrass Grassland
	G. Lignum – Glinus Shrubland
	H. Poplar Box – Black Box Woodland

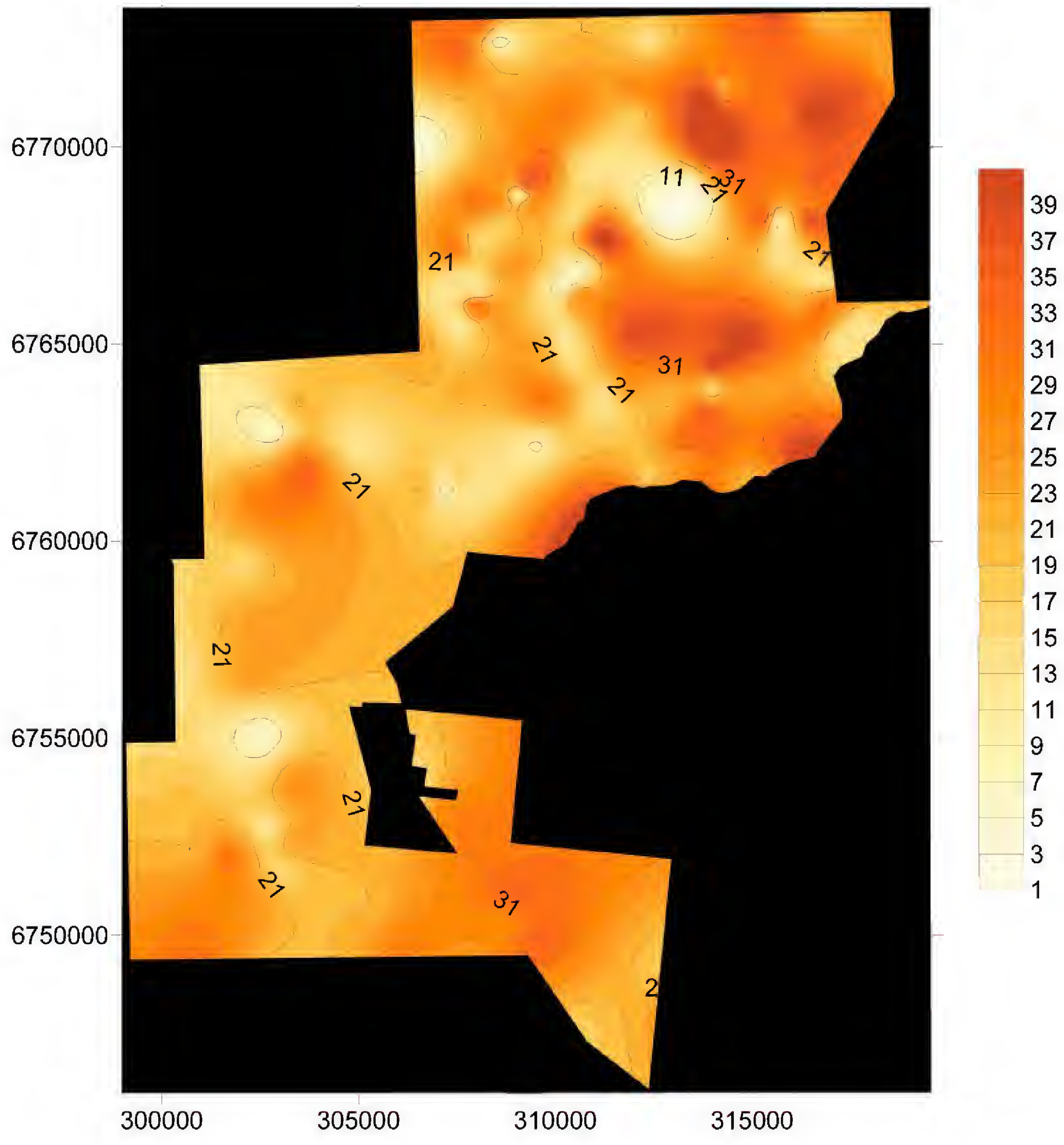

Figure 1: Modelled relative abundance of contemporary Aboriginal flora resources within *Naree* and *Yantabulla* stations. X and Y co-ordinates refer to eastings and northings within Zone 54, Datum 94.

Results

Of the 355 native vascular plant species found in the *Naree* and *Yantabulla* study area, 130 (37%) have been recorded as being used in some form by indigenous peoples (see Appendix 1). Of these 91 had been used for food, 58 medicinally, 33 for tools and only 10 ceremonially. Forbs, followed by shrubs and then grasses and trees were the most used species in the study region (Table 2).The difference between high and low plant resource locations is nearly forty-fold (Figure 1). There is no relationship between defined floristic Groups or Alliances and plant resource use scores (Figures 2 & 3). Overall, Lignum areas (G) (Figure 3) had the lowest resource use score range. A power function relationship accounted for 42% (Figure 4) of the variation between species density (richness per plot) and Aboriginal plant resource score.

Table 2: Distribution of Aboriginal usage plants from *Naree* and *Yantabulla* Stations by major plant life form categories.

Life Form	Richness
Fern	1
Forb	54
Grass	18
Hemi-parasite	5
Shrub	30
Tree	16
Vine	4

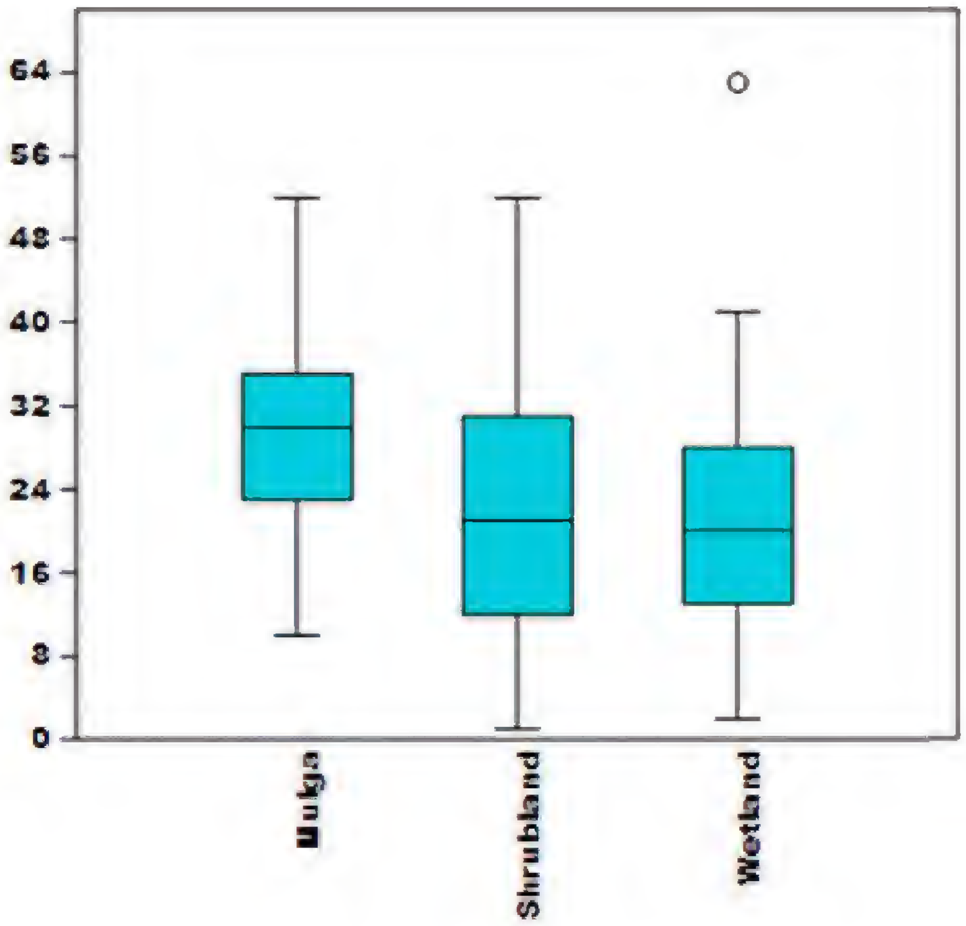

Figure 2: Comparison of relative abundance of Aboriginal flora resources within the floristic Groups of Hunter and Hunter (2016). There is no significant difference in resources between major floristic groups.

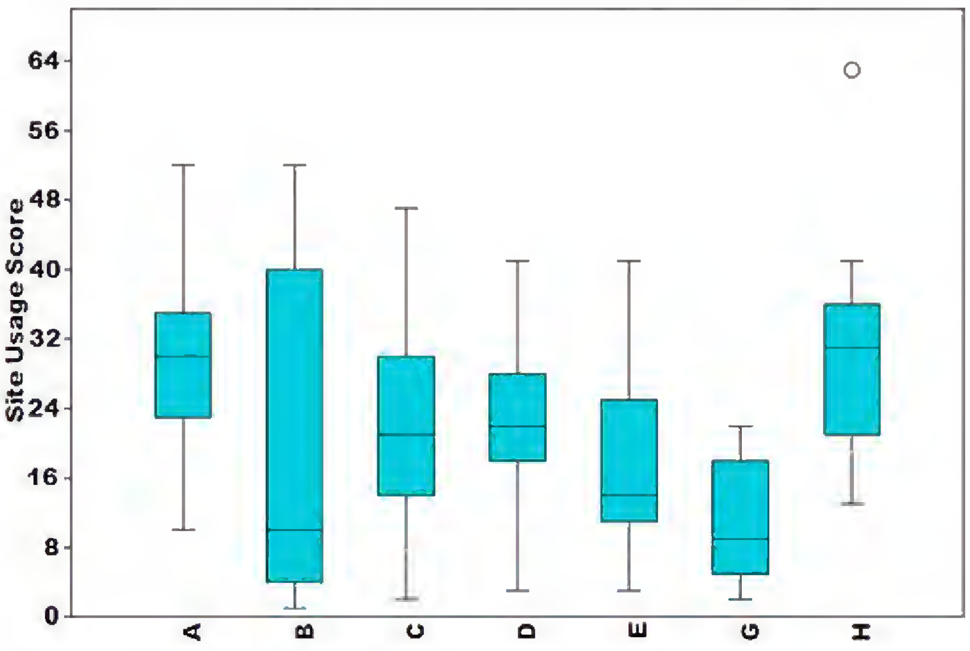

Figure 3: Comparison of relative abundance of Aboriginal flora resources within the floristic Alliances of Hunter and Hunter (2016). There is no significant difference in resources between floristic group Alliances. See Table 1 for titles of floristic Alliances.

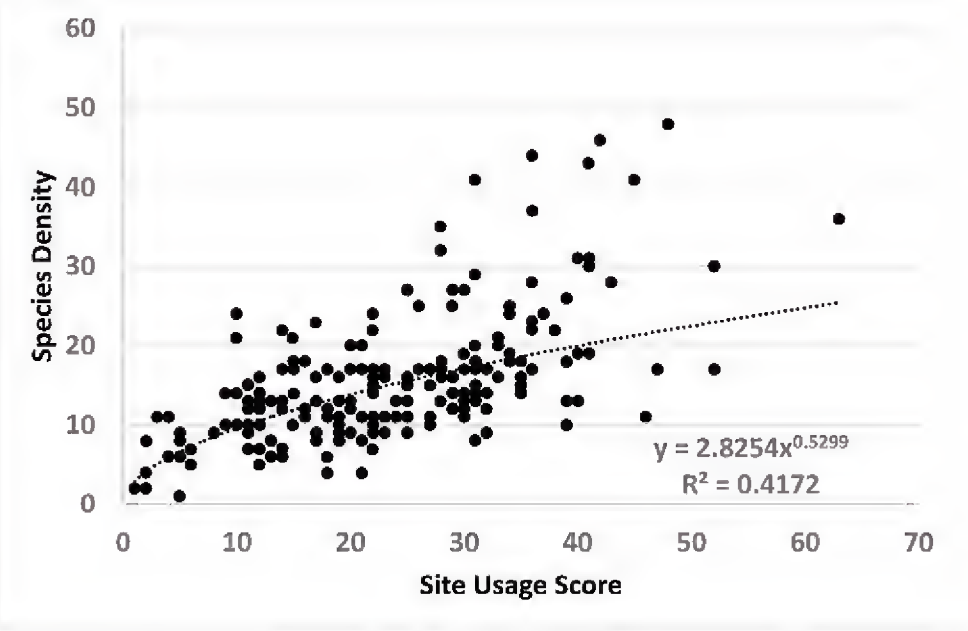

Figure 4: Power relationship between site species richness (species density) and site usage score.

Discussion

The results show that Aboriginal plant resources are heterogeneously distributed across the *Naree* and *Yantabulla* landscape in north western New South Wales. Peaks in useful plant materials are nearly 40 times greater than troughs in the landscape, but these were not found to coincide with phytosociological units defined by floristic analysis (Hunter & Hunter 2016). Thus, general vegetation mapping of plant community types cannot be used to infer high or low Aboriginal plant use abundance locations in our study region. Nor are areas of high and low Aboriginal plant usage clearly associated with major landscape features such as wetland areas, escarpment or dune systems at our scale of analysis.

High congruence between species rich locations and high Aboriginal plant use was found, indicating that enhancing and/or protecting areas of high natural plant species richness is also likely to assist in protecting areas of cultural importance within the landscape though it is acknowledged that not all Aboriginal groups used the same plants, or used them in the same ways. Furthermore, we acknowledge that plant resources important to Aboriginal peoples are only one aspect of culturally significant areas, and that locations of high fauna food resources, or areas of spiritual importance, have not been taken into account. However, it is hoped that by identifying contemporary high resource locations new understandings of the landscape can be developed by traditional owners and conservation land managers.

Acknowledgements

The authors wish to thank Vanessa Hunter, Dana Vickers and Sandy Gilmour for assistance in the field. Bush Heritage Australia and South Endeavour Trust are thanked for allowing access to their lands. David and Sue Akers, managers of *Naree* and *Yantabulla* are also thanked for facilitating and assisting in all areas of this investigation. Karen Martin-Stone is thanked for making comments on a previous draft.

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Appendix 1

Native plant species on *Naree* and *Yantabulla* stations and reported use to Aboriginal peoples (as food, medicine, tools or ceremonial).

Sources - Maiden 1889; Henshall *et al.* 1980; Cunningham *et al.* 1981; Levitt 1981; Cribb & Cribb 1982; Leiper & Houser 1984; Goddard & Kalotas 1985; Low 1985; Cribb & Cribb 1986; Low 1988; Low 1989; Low 1990; Wightman & Smith 1989; Smith & Wightman 1990; Wightman *et al.* 1991; Wightman *et al.* 1992ab; Zola & Gott 1992; Lazarides & Hince 1993; Leiper & Houser 1993; Latz 1995; Bindon 1996; Stewart & Percival 1997; Maslin *et al.* 1998; Harris *et al.* 2000; Lassack & McCarthy 2011; McKerney & White 2011; Williams 2011.

Species	Food	Medicine	Tools	Ceremonial
Abutilon leucopetalum	1			
Abutilon otocarpum	1			
Acacia aneura	1	1	1	1
Acacia brachystachya	1			
Acacia excelsa	1	1	1	
Acacia oswaldii	1		1	
Acacia ramulosa	1			
Acacia stenophylla	1			
Acacia tetragonophylla	1		1	
Acacia victoriae	1		1	
Alectryon oleifolius	1		1	
Alstonia constricta		1		
Amaranthus grandiflorus	1			
Amaranthus macrocarpus	1			
Amphipogon caricinus			1	
Amyema cambagei	1			
Amyema lucasii	1			
Amyema maidenii	1			
Atalaya hemiglauca	1			1
Atriplex elachophylla		1		
Boerhavia coccinea	1			
Boerhavia dominii	1	1		
Boerhavia repleta	1			
Brachychiton populneus	1		1	
Bulbine alata	1			
Calandrinia eremaea	1			
Callitris glaucophylla	1	1	1	
Calostemma purpureum	1		1	
Capparis mitchellii	1	1		
Casuarina pauper			1	1
Centipeda cunninghamii		1		
Centipeda minima		1		
Centipeda thespidioides		1		
Chamaesyce drummondii		1		
Chenopodium auricomum	1			
Chenopodium cristatum		1		
Chenopodium melanocarpum		1		
Citrullus lanatus	1			
Cymbopogon ambiguus		1		
Cyperus bifax		1		
Dactyloctenium radulans	1			
Dianella porracea	1		1	
Dodonaea viscosa		1	1	
Duma florulenta	1		1	
Dysphania kalpari	1	1		
Dysphania rhadinostachya	1	1		
Echinochloa inundata	1			
Einadia hastata	1			
Einadia nutans	1		1	
Enchylaena tomentosa	1	1	1	
Enteropogon acicularis			1	
Eragrostis australasica	1			
Eragrostis basedowii	1			
Eragrostis dielsii	1			
Eragrostis eriopoda	1			1
Eragrostis kennedyae	1			
Eragrostis lacunaria	1			
Eragrostis laniflora	1			
Eragrostis leptocarpa	1			
Eragrostis setifolia	1			
Eremophila bignoniiflora		1		1
Eremophila deserti	1			
Eremophila gilesii		1		
Eremophila latrobei		1		
Eremophila longifolia	1	1		1
Eremophila mitchellii	1	1	1	
Eremophila sturtii		1		
Erodium crinitum	1			
Eucalyptus coolabah	1	1	1	
Eucalyptus largiflorens	1		1	1
Eucalyptus melanophloia		1	1	
Eucalyptus populnea	1	1	1	
Flindersia maculosa	1	1	1	
Goodenia lunata			1	
Grevillea striata	1	1	1	
Hakea eryeana		1		
Hakea leucoptera	1	1		
Hakea tephrosperma	1			1
Linum marginale	1		1	
Lysiana exocarpi	1			
Lysiana subfalcata	1			
Malva parviflora		1		
Marsdenia viridiflora	1			
Marsilea drummondii	1			
Marsilea hirsuta	1			
Myoporum montanum	1	1	1	

Species	**Food**	**Medicine**	**Tools**	**Ceremonial**
Owenia acidula	1	1		
Panicum decompositum	1			
Panicum effusum	1			
Phyllanthus lacunarius		1		
Phyllanthus virgatus		1		
Pimelea microcephala	1	1		
Pluchea tetranthera		1		
Portulaca oleracea	1	1		
Pseudognaphalium luteoalbum		1		
Psydrax latifolium	1			
Pterocaulon sphacelatum		1		
Santalum acuminatum	1	1	1	
Scaevola spinescens		1		
Schoenoplectus laevis	1			
Senna artimisioides subsp. *filifolia*		1		
Senna artimisioides subsp. *x sturtii*		1		
Sida goniocarpa	1			
Sida platycalyx	1		1	
Solanum cleistogamum	1	1		
Solanum coactiliferum	1			
Solanum ellipticum	1			
Solanum esuriale	1			
Sonchus oleraceus	1	1		
Themeda avenacea	1	1		
Themeda triandra	1			
Trachymene glaucifolia	1			
Trachymene ochracea	1			
Tribulus terrestris	1			
Ventilago viminalis	1	1	1	
Wahlenbergia gracilis	1			
Zygophyllum iodocarpum	1			

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The first record of the endangered fern *Hypolepis distans* Hook. (Dennstaedtiaceae) on the Australian mainland

Kevin Mills

Jamberoo, NSW AUSTRALIA. Email kevinmillskma@gmail.com

***Abstract*:** The terrestrial fern *Hypolepis distans* (Dennstaedtiaceae) is recorded as indigenous to New Zealand and Tasmania. The fern was not known from New South Wales or the Australian mainland until recently. This paper reports on the recent discovery of the species at Macquarie Pass in the Illawarra area on the south-eastern edge of the Central Tablelands Botanical Subdivision of New South Wales. Its ecology and conservation needs are discussed.

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Introduction

The terrestrial fern *Hypolepis distans* (family Dennstaedtiaceae), commonly known as Scrambling Ground Fern, is recorded as indigenous to New Zealand and Tasmania. During a survey as part of a regional study of the fern flora on the NSW south coast, a colony of *Hypolepis distans* was located in the vicinity of Macquarie Pass, about 29 kilometres southwest of the City of Wollongong, on the extreme south-eastern edge of the New South Wales Central Tablelands Botanical Subdivision. The recent collection of the fern from the Central Tablelands is the first for that state and the first for the Australian mainland. This paper documents the discovery and discusses the habitat and conservation implications.

The Species *Hypolepis distans*

The species was named by Joseph Hooker in his treatise on ferns *Species Filicum* (Hooker 1858). The fern is known from the northwest corner of Tasmania and on King Island (Garrett 1996), 110 kilometres to the north. In New Zealand it is widespread, including the Chatham Islands (Brownsey & Smith-Dodsworth 2000). The first record of *Hypolepis distans* in Australia was from King Island in 1973 (Chinnock 1976); the species was subsequently discovered in northwest Tasmania. The total population in Tasmania and King Island is very small, nine confirmed populations containing a total of 500-1000 plants (Threatened Species Section Tasmania 2012).

The only other place that *Hypolepis distans* is known to occur is Norfolk Island, the result of an unintentional introduction, where it grows in a limited area, and is removed as an unwanted introduction (de Lange & Christian 2000). It is clear in this case that the species was introduced in peat moss from New Zealand used in the Forestry Nursery, where the plants were found (de Lange & Christian 2000). The possibility of the Australian plants in Tasmania also being introduced in peat moss is discussed by these authors, although they do not take a stand on the matter either way.

The scrambling habit of *Hypolepis distans* makes it distinct from other species in *Hypolepis*; this has been noted by Brownsey (1983). Brownsey and Chinnock (1987) noted that "*Hypolepis distans* can be distinguished immediately from all other species [of *Hypolepis*] by its relatively long, narrow frond, the pinnae arising in opposite or subopposite pairs at right angles to the rachis, the veins ending in emarginations..., the thin, highly polished, rather brittle stipe and the dark brown spores with virtually no perispore projections..."

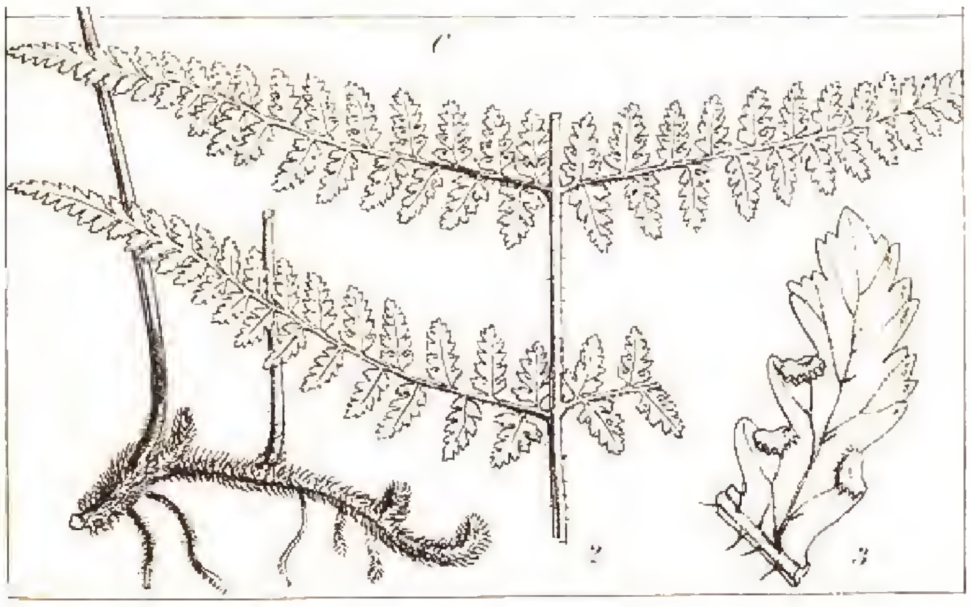

Figure 1: Hooker's plate of *Hypolepis distans* from *Species Filicum* (Hooker 1858).

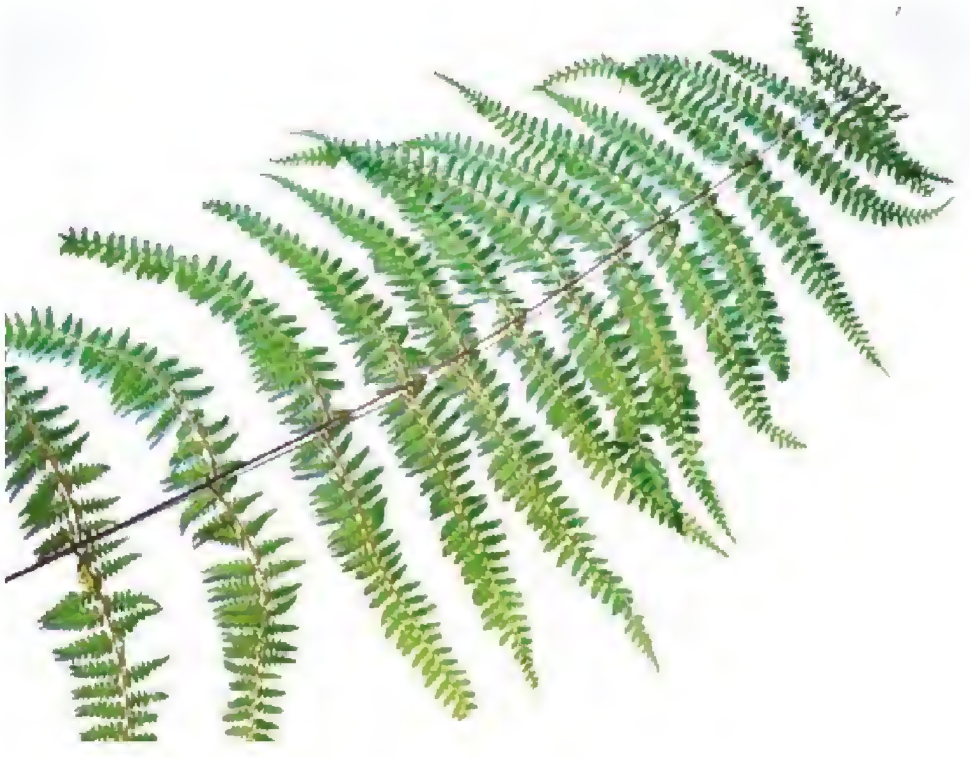

Figure 2: Frond of *Hypolepis distans* from the Macquarie Pass site. Note well spaced, opposite pinnae arising at right angles to rachis.

Conservation Status

Hypolepis distans is listed under Commonwealth legislation as Endangered (*Environment Protection and Biodiversity Conservation Act 1999*), as it is only known from a handful of Australian sites in Tasmania and on King Island (Garrett 1996). The species is not threatened in New Zealand, where it is quite widespread (Brownsey & Smith-Dodsworth 2000). In Tasmania the species is currently listed as Endangered under the Tasmanian Government *Threatened Species Protection Act 1995* (Tasmania 1995) due to its narrow occurrence and relatively low number of plants. Given its rarity in New South Wales, this fern is a candidate for listing as a critically endangered species under the NSW *Biodiversity Conservation Act 2016 (NSW 2016)*.

The new record for New South Wales

In June 2017 a colony of *Hypolepis distans* was found in the Macquarie Pass area, west of Kiama in the Central Tablelands Botanical Subdivision of New South Wales. The occurrence is over 800 km northeast of the nearest other Australian occurrence, on King Island in Bass Strait, to the northwest of Tasmania, and about 2000 kilometres west of the closest occurrence in New Zealand. Although some vegetation studies have previously been undertaken in the area (e.g. Fallding & Benson 1985), little detailed survey has been done on the plants of the Macquarie Pass area, although the recent study by Mills (2017) carried out extensive surveys of the fern flora, one outcome being this discovery of *Hypolepis distans*. The species has not been found in the nearby upper Minnamurra River catchment, despite a history of fern interest and identification by Minnamurra Falls Reserve ranger Howard Judd in the 1950s-70s, and more recently by Mills (2016). It is very likely that this fern has been present for quite some time, and being in a rather inaccessible location to the public and botanists alike, had not been found.

The colony of *Hypolepis distans* was found in two sites near Macquarie Pass National Park, on a high plateau at an altitude of about 620 m. The exact locations of the two sites are purposefully withheld. The sites are within semi-cleared tall eucalypt forest growing on the Hawkesbury Sandstone just below the boundary with the overlying Wianamatta Group shale. The sites are on gentle south-facing slopes about 400 m apart; both are associated with a significant outcrop of sandstone. The extent of each site is small; 40 m by 20 m and 5 m by 2 m. The number of plants present is unable to be determined as their intertwined rhizomes and tangle of fronds make identification of individual plants impossible. A second visit to the location in September 2017 found that most of the fronds on the taller plants were dead, likely the result of winter frosts; smaller plants seemed to be unaffected.

The soil is a deep loam with much sand, and high in organic matter; the sites are rather poorly drained due to underlying sandstone, but not the swampy habitat mentioned in the literature for Tasmania and New Zealand.

The surrounding forest is dominated by very tall *Eucalyptus smithii* trees with occasional *Eucalyptus fastigata*; the understorey is mostly cleared. The non-fern understorey species include scattered small trees of *Acacia melanoxylon, Tristaniopsis collina* and *Doryphora sassafras*, and the creeper *Hibbertia scandens*. Ferns are very prominent on the sites, including *Blechnum wattsii, Dicksonia antarctica, Histiopteris incisa, Hypolepis glandulifera, Pteridium esculentum, Sticherus flabellatus, Todea barbara,* and, epiphytic on the sandstone, *Hymenophyllum cupressiforme, Notogrammitis billardierei* and *Pyrrosia rupestris*. The first six of these ferns are also associated with the Tasmanian population (Threatened Species Section Tasmania 2012, p.44). Specimens have been lodged with the National Herbarium of NSW, Sydney (NSW), where the identity of the species was confirmed. Fertile fronds were present in June 2017.

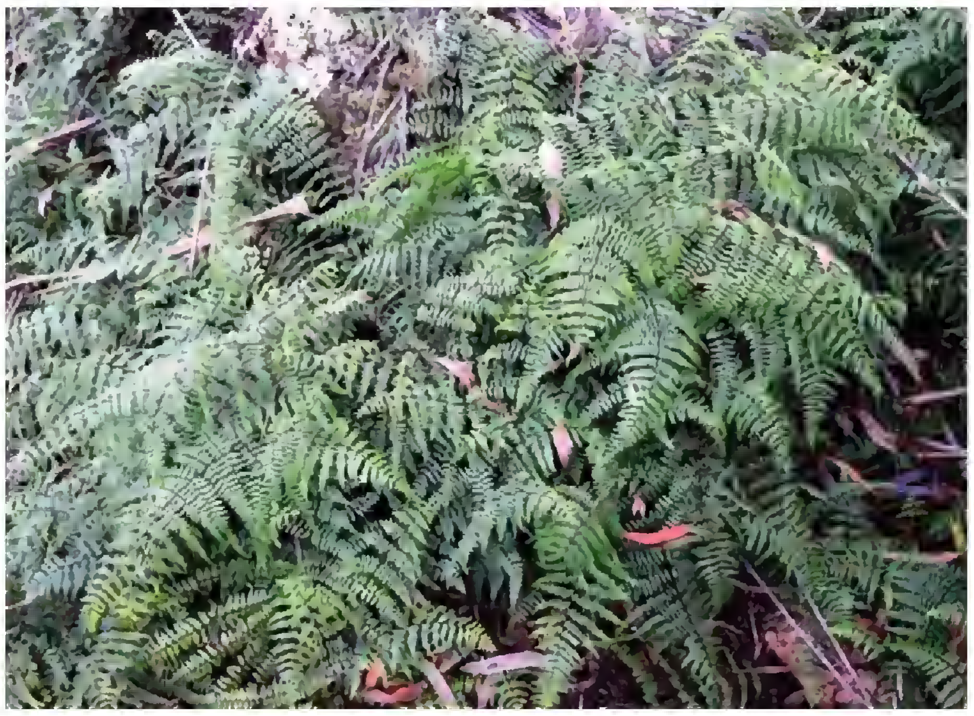

Figure 3: Part of the colony of *Hypolepis distans* at the Macquarie Pass site, photographed June 2017.

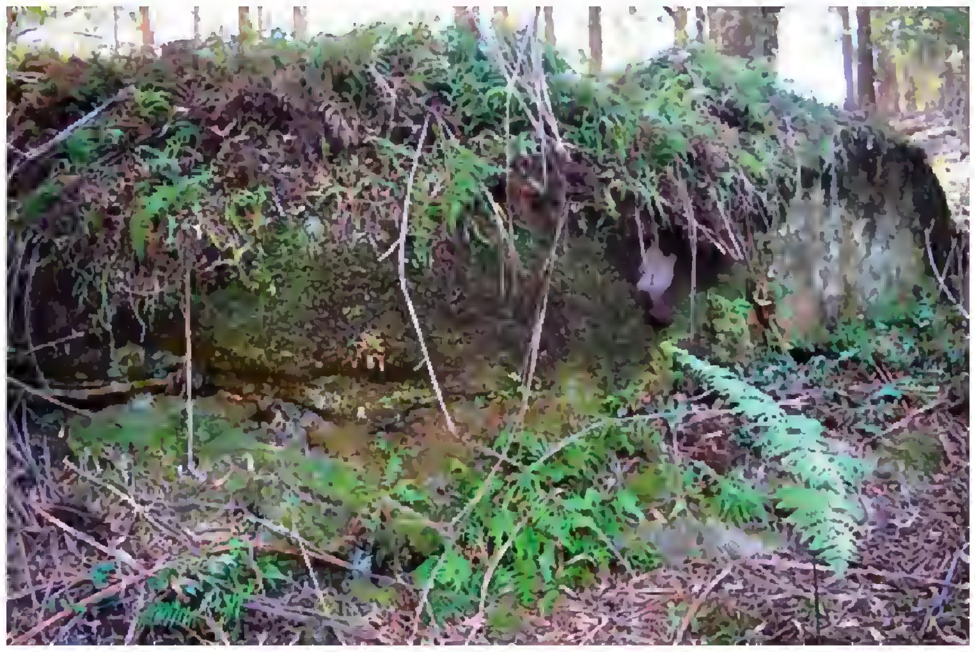

Figure 4: Habitat of *Hypolepis distans* at Macquarie Pass; note plants above and below the sandstone outcrop. Larger fern lower right is *Histiopteris incisa*.

Discussion

To find New Zealand species in Australia is not very common. Because the weather systems move from west to east, there is much greater opportunity for Australian species to move in the opposite direction. Distance is not necessarily a barrier to fern dispersal; ferns have fine spores that can travel great distances on the wind and explains the wide distribution of many species.

The question of the origin of the species at Macquarie Pass requires consideration. The possibility of an introduction through imported peat moss (as at Norfolk Island) to two widely separated Australian locations (Tasmania and NSW), neither of which is near habitation, seems rather remote. The Tasmanian occurrence is considered to be indigenous, and the author takes the view that the species is also indigenous to

New South Wales, and an unusual natural introduction from New Zealand, probably well before European colonisation.

The species is a potential candidate for listing as Critically Endangered under the New South Wales threatened species legislation; a proposal has been submitted to the NSW Scientific Committee by the author. The Macquarie Pass occurrence requires conservation action as the site is semi-cleared forest in a grazing paddock. Only a few plants occur in the nearby Macquarie Pass National Park and liaison between the landowners and the NSW National Parks and Wildlife Service is essential to ensure the conservation of this population.

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